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RECRUITMENT, POST-METAMORPHIC DRIFTING AND REPRODUCTIVE OUTPUT IN THE HERBIVOROUS GASTROPOD *LACUNA* SPP. WITHIN KELP CANOPIES AND INTERTIDAL SEAWEED COMMUNITIES

by

ANDRE MARTEL ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
Fall 1990

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled RECRUITMENT, POST-METAMORPHIC DRIFTING AND REPRODUCTIVE OUTPUT IN THE HERBIVOROUS GASTROPOD LACUNA SPP. WITHIN KELP CANOPIES AND INTERTIDAL SEAWEED COMMUNITIES submitted by ANDRE MARTEL in partial fulfillment of the requirements of the degree of DOCTOR OF PHILOSOPHY

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ABSTRACT

Pre- and post-settlement factors controlling recruitment of the herbivorous gastropod Lacuna vincta in the canopies of Macrocystis and Nereocystis beds were studied. These factors encompass seasonality of oviposition, larval abundance, in situ larval growth, larval settlement and juvenile migration. Egg masses and adults are abundant on low intertidal algae but are seldom observed in Macrocystis and Nereocystis canopies. The study of cohorts of larvae enabled the determination of the planktonic period (7-9 weeks) as well as the forecasting of timing and intensity of recruitment. Recruitment rates in kelp canopies coincided with patterns of abundance of advanced larvae (>500 µm) in the plankton. Newly-metamorphosed juvenile L. vincta consistently dominate the canopy and observations suggest that shortly after metamorphosis they migrate, via drifting, to the undercanopy or low intertidal area. It is hypothesized that factors such as lack of shelter and increased vulnerability to fish predation are selective pressures favoring this habitat shift. A similar pattern of habitat use by juvenile stages of other benthic invertebrates is reported.

Quantitative evidence that several marine benthic invertebrates lacking a planktonic larval stage disperse as juveniles and small adults by drifting in the water column was obtained using off-bottom collectors that mimicked a habitat used by many small molluscs in the intertidal. It is

shown that Lacuna can voluntarily produce a mucous thread and initiate drifting. Mucous threads not only reduce sinking rates, but also enhance the animal's ability to attach to nearby substrata. The ultrastructure of drifting mucous threads is described.

Finally, recruitment and population dynamics of Lacuna spp. in semi-exposed rocky intertidal seaweed communities, as well as the significance of post-metamorphic drifting and plant morphology on temporal and spatial patterns of abundance of the snails were investigated. It is shown that substratum (algae) choice by juvenile and even adult L. vincta during drifting has significant implications for life-history parameters, including growth, sexual dimorphism, maximum size and, more importantly, fecundity. Females that drift from certain algae which were originally selected at settlement can markedly increase their egg production and lifetime fecundity by colonizing other seaweeds (such as kelp).

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CHAPTER I.

GENERAL INTRODUCTION

During the last few years there has been a resurgence of interest among marine scientists in factors controlling the earliest appearance of juveniles within populations of benthic marine invertebrates (see Young [1987] for a reconsideration of the novelty of "supply-side" ecology). Factors that regulate recruitment include pre-settlement parameters that affect supply of larvae as well as post-settlement events that influence density and distribution of juveniles (Cameron and Schroeter, 1980; Cameron and Rumrill, 1982; Keough and Downes, 1982; Connell, 1985). The supply of early juvenile stages to established populations constitutes a determinant of community structure in marine benthic invertebrates (Underwood and Denley, 1984; Connell, 1985).

Recruitment in benthic marine invertebrates has been defined as the presence of the smallest age-group of juveniles that can be accurately censused by an observer in a population survey (Connell, 1985). Pre-settlement events that govern recruitment include (1) oceanographical and biological processes that affect spatial distribution of larvae in the plankton (Cameron and Rumrill, 1982; Grosberg, 1982; Legendre and Demers, 1984; Young and Chia, 1989), (2) larval mortality (Rumrill et al., 1985; Rumrill, 1987), (3) abundance and availability of competent larvae present in the settling area (Grosberg, 1982; Yoshioka, 1982; Gaines and

Roughgarden, 1985; Crigg, 1988) and (4) settlement behaviour (Barker, 1977; Highsmith, 1982; Young and Chia, 1982; Chia *et al*., 1984; Davis, 1987; Rowley, 1989). However, because of the numerous sources of variability occurring during the planktonic larval period, few studies have successfully integrated data on timing of release of larvae, *in situ* larval growth, temporal patterns of abundance of competent larvae in the plankton, as well as settlement rates in order to forecast timing and intensity of recruitment.

Patterns of abundance and distribution of early juveniles are also influenced by factors that take place following larval settlement and metamorphosis. Among these post-metamorphic events, juvenile mortality and migration are of paramount importance. Many authors have identified early juvenile mortality as a crucial factor determining the intensity of recruitment in several phyla of benthic marine invertebrates (Cameron and Schroeter, 1980; Keough and Downes, 1982; Luckenbach, 1984; Young and Chia, 1984; Andrew and Choat, 1985; Connell, 1985; Jensen and Jensen, 1985; Davis, 1987; Rowley, 1989). In contrast, post-metamorphic migrations have received comparatively little attention, despite their potential for influencing patterns of abundance and distribution for both juveniles and adults (Young and Chia, 1982; Chia *et al*., 1984).

A. ECOLOGICAL SIGNIFICANCE OF POST-METAMORPHIC MIGRATION AND DRIFTING IN MOLLUSCS

Displacement of post-metamorphic stages can play a crucial role in the life history of many molluscs (Bayne, 1964; Sigurdsson *et al*., 1976, Sigurdsson, 1980). One mechanism of dispersal involves passive drifting of post-larval and juvenile stages in the water column (see Highsmith [1985] for alternative methods of dispersal). Dispersal of post-metamorphic stages has been particularly well documented in bivalves. Post-larval bivalves use specialized drifting byssal threads secreted by specific glands in the foot (de Block and Tan-Mass, 1977; Lane *et al*., 1982, 1985). These byssal threads can be many times the length of the animal itself and act as a sea anchor or "sail", enabling the individual to be carried passively by water currents (see Prezant and Charlermwat, 1984).

Dispersal of post-larvae and juveniles can play a key role in the recruitment of certain molluscs. Bayne (1964) demonstrated that juvenile *Mytilus edulis* can disperse to habitats different from those originally selected by larvae at settlement. Most individual *M. edulis* that were observed to recruit to adult mussel beds were juveniles rather than larvae (Bayne, 1964). More recently, Beukema and de Vlas (1989) demonstrated a similar pattern of recruitment in the clam *Macoma balthica* in the North Sea.

Despite its widespread occurrence in marine molluscs, the role of post-metamorphic drifting in the recruitment process has not been determined for the majority of species. Furthermore, questions concerning relationships between the initiation of drifting and voluntary behavioural traits have not been addressed. Moreover, few investigators have focused on the consequences of substratum choice made by post-metamorphic stages on life-history parameters such as growth and fecundity.

B. APPLICATION OF THE LACUNA SYSTEM TO STUDIES OF RECRUITMENT AND POST-METAMORPHIC DRIFTING

Small herbivorous gastropods of the genus *Lacuna* have been the object of several studies on population biology conducted along the coasts of England (Smith, 1973; Southgate, 1982; Grahame, 1986) and California (Langan, 1984). *Lacuna* spp. often occur in large numbers on subtidal and intertidal algae (Fralick *et al*., 1974; Smith *et al*., 1985; Johnson and Mann, 1986). *Lacuna* spp. veligers settle upon a variety of macroalgal substrata (Fretter and Manly, 1977), and newly-metamorphosed juveniles are large enough (750-850 um) to be censused in the field by an observer. These characteristics enable recruitment assessments immediately after larval metamorphosis (see Connell, 1985). Sampling is further facilitated since individuals of *Lacuna* spp. live and feed on seaweeds; thus, both the substratum and the animals can be brought into the laboratory for quantitative analysis. As a consequence, the *Lacuna* spp. system is particularly suitable for investigations of recruitment. Recent studies have reported that these gastropods are highly adapted to drifting in the water column (Johnson and Mann, 1986; Martel, 1987, 1988). Thus, Lacuna spp. provide an opportunity to investigate the impact of post-metamorphic drifting on recruitment patterns of benthic marine invertebrates.

Lacuna spp. are easy to raise in the laboratory on the various algae on which they occur in the field, individuals spawn within 3-4 months after metamorphosis, and they have a life-span of only one year. It is therefore possible to test for effects of substratum choice (algae) made by drifting snails on life-history parameters such as growth and reproductive output. This system thus gives the investigator the rare opportunity to study the life-time fecundity of a marine benthic invertebrate (see Miller and Hadfield, 1990).

C. OBJECTIVES AND QUESTIONS ADDRESSED

The objectives of the present thesis are: (1) to report the recruitment of the herbivorous gastropod Lacuna spp. in kelp beds and rocky intertidal seaweed communities, with emphasis on the relative importance of post-metamorphic drifting and migration; (2) to demonstrate that the ability of individuals to disperse in the water column and relocate to other substrata can represent an adaptation in sessile or sedentary species whose habitat is short-lived and whose life history includes ontogenetic changes in habitat use; and (3) to demonstrate that drifting excursions and relocation in new habitats can result in enhanced reproductive output.

Specific questions addressed in the thesis include: (1) what role does post-metamorphic drifting play in the recruitment of Lacuna spp.? (2) is initiation of drifting the result of a voluntary response from the snail? (3) does post-metamorphic drifting play an important role in the dispersal of species lacking a planktonic larval stage? (4) what is the biological function and ultrastructure of drifting mucous threads? (5) what are the consequences of habitat choice made during drifting on snail growth and fecundity? and (6) is there evidence to indicate that post-metamorphic drifting is adaptive?

D. ORGANIZATION OF THE THESIS

The thesis is composed of three main chapters (II, III, IV). Chapter II investigates recruitment of the herbivorous gastropod Lacuna vincta within kelp bed canopies (Macrocystis integrifolia and Nereocystis luetkeana) in Barkley Sound, Vancouver Island, British Columbia. The study focuses on factors influencing intensity and patterns of recruitment, by examining periods of oviposition, growth of planktonic larvae in the field, abundance of competent larvae and their settlement in kelp bed canopies. Results of the study demonstrate that it is possible to obtain an accurate in situ estimate of the duration of the planktonic period, and also to forecast the timing and intensity of recruitment. The study also shows that juvenile L. vincta disappear from the canopy habitat shortly after larval recruitment. It is hypothesized that kelp bed canopies act as larval collectors and may be used as a nursery before animals migrate via drifting towards the undercanopy and low intertidal seaweeds. The adaptive significance of the initiation of dispersal is discussed in light of possible increased vulnerability to fish predation occurring during ontogeny. In addition, I report a similar pattern of habitat (canopy) use by another gastropod (*Alia* [=*Mitrella*] *gouldi*) as well as by an unidentified asteroid echinoderm.

In Chapter III, I examine the significance of post-metamorphic drifting in several intertidal molluscs that lack a planktonic larval stage. Results demonstrate that several widely distributed species (primarily bivalves and gastropods) can disperse as juveniles and small adults by drifting in the water column. Evidence for this phenomenon comes from the use of off-bottom intertidal collectors that were mimics of an important habitat used by these small invertebrates: red turf algae. This study also confirms that the initiation of drifting can be controlled by the snail (at least for *Lacuna* spp.). I also investigate the biological properties and structure of drifting mucous threads. Their structure is compared with that of attachment threads produced by a non-drifting gastropod found in similar habitats.

Chapter IV consists of two main sections, the first of which presents the results of a 30-month recruitment study of

Lacuna variegata and *L. vincta* living in semi-exposed rocky intertidal seaweed communities. Emphasis is placed on the significance of plant morphology and juvenile drifting as two primary factors influencing patterns of distribution and abundance of these snails. In the second section of Chapter IV, I examine the consequences of algal choice (diet) by settling larvae, drifting juveniles and adults on growth and reproductive output of adults. Results from algal choice experiments strongly support the hypothesis that the ability of post-metamorphic stages of *Lacuna* spp. to disperse by drifting in the water column and relocate to other seaweeds after settlement has favourable consequences regarding maximum adult size and egg production.

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CHAPTER II.

OVIPOSITION, LARVAL ABUNDANCE AND RECRUITMENT OF THE HERBIVOROUS GASTROPOD LACUNA VINCTA (MONTAGU) WITHIN KELP CANOPIES [1]

A. INTRODUCTION

Larval recruitment is a key mechanism influencing the structure and dynamics of populations of marine benthic invertebrates (Underwood and Denley, 1984; Connell, 1985; Gaines and Roughgarden, 1985). Recruitment is determined by events occurring at different stages in the life cycle, including (1) spawning success (release and fertilization of gametes or deposition of egg masses), (2) supply of metamorphically competent larvae, (3) settlement rate and (4) post-metamorphic events, including juvenile survival and migration (Barker, 1979; Cameron and Schroeter, 1980; Cameron and Rumrill, 1982; Keough and Downes, 1982; Yoshioka, 1982; Young and Chia, 1982, 1984; Chia *et al*., 1984; Underwood and Denley, 1984; Gaines and Roughgarden, 1985; Davis, 1987; Rowley, 1989). Moreover, planktonic larvae are subject to biological and oceanographical processes which contribute to spatial and temporal variability in the abundance of competent larvae metamorphosing in the adult habitat

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[1] A version of this chapter has been submitted to **Marine Biology** for publication. Martel, A., Chia, F. S.. Oviposition, larval abundance and recruitment of the herbivorous gastropod *Lacuna vincta* (Montagu) within kelp bed canopies.

(Cameron and Rumrill, 1982; Grosberg, 1982; Legendre and Demers, 1984; Gaines et al., 1985; Ebert and Russell, 1988; Rumrill, 1989). The complexity of the interactions between these variables during the planktonic larval stage explains, at least in part, the scope of difficulties related to the quantitative study of recruitment in marine organisms.

Most studies of recruitment in benthic marine invertebrates have dealt with sessile organisms (Bernstein and Jung, 1979; Yoshioka, 1982; Keoughs and Downes, 1982; Gaines and Roughgarden, 1985; Connell, 1985; Davis, 1987). In such systems the absence of juvenile displacement facilitates monitoring recruitment. Other studies have examined recruitment in non-sessile invertebrates (Fretter and Manly, 1977; Barker, 1977; Sarver, 1979; Cameron and Schroeter, 1980; Rowley, 1989). Cameron and Rumrill (1982) have investigated the patterns of larval abundance and recruitment in the sand dollar Dendraster excentricus. More recently, Rumrill (1987, 1989) evaluated pre-and post-settlement factors that influence patterns of recruitment in the asteroid Asterina miniata.

To date, research has shown that invertebrate communities living in the Macrocystis canopy are primarily composed of sessile species, such as bryozoans, hydroids and serpulid polychaetes (Bernstein and Jung, 1979; Yoshioka, 1982). However, I have found that, on the west coast of Vancouver Island, the Macrocystis canopy is one of the habitats used extensively for settlement by the larvae of a non-sessile invertebrate, the herbivorous gastropod *Lacuna vincta*. Thus, the first objective of the present study is to describe the pattern of recruitment of this prosobranch in the canopies of *Macrocystis integrifolia* and *Nereocystis luetkeana* beds. An assessment of the recruitment pattern of *L. vincta* has been achieved by integrating quantitative data on oviposition, larval abundance, larval growth in the plankton and settlement, over a 30-month period.

The use of specific habitats by juveniles can result in differential distribution among the various age groups of a population. Such age- or size-specific patterns of habitat use have been observed in many marine invertebrates (Marx & Herrnkind, 1985; Herrnkind and Butler, 1986; Kneib, 1987 a, b; Orth & van Montfrans, 1987). Juveniles occupying a nursery ground must eventually migrate to the adult habitat. For benthic invertebrates like molluscs, this movement could be accomplished by crawling. Other means of translocation have, however, been observed among small marine benthic invertebrates. Juvenile dispersal by drifting in the water column has been reported in bivalves (Bayne, 1964; Sirgurdsson *et al*., 1976; Beukema and de Vlas, 1989) and gastropods (Vahl, 1983; Johnson and Mann, 1986; Lane *et al*., 1985; Martel, 1987, 1988). Drifting by molluscs usually involves the use of specialized foot secretions (byssal or mucous threads), which act like a sea anchor by reducing sinking rates.

The second part of this study was initiated following field observations which revealed that the recruitment of the herbivorous prosobranch *Lacuna vincta* into *Macrocystis* and *Nereocystis* canopies never leads to adult populations in this habitat. It aims to demonstrate that the likely explanation for the disappearance of juvenile *L. vincta* following settlement and metamorphosis is a migration of juveniles from the canopy to the undercanopy or to a low intertidal habitat. Direct observations (SCUBA), the use of off-bottom collectors and the study of size-frequency distributions of individuals at the time of recruitment contributed to a better understanding of this movement. Fish stomach content analyses and laboratory experiments on predation, permit me to hypothesize that the initiation of this migration of juvenile *L. vincta* is an adaptive response to increased vulnerability to fish predation. In addition, I report that the *Macrocystis* canopy is utilized by the larvae and newly-metamorphosed juveniles of other non-sessile invertebrates found in *Macrocystis* beds, such as the neogastropod *Alia* (=*Mitrella*) sp. and one, possibly two, asteroid species. I also show the importance of kelp canopies as a potential nursery habitat for many species of benthic invertebrates and stress the significance of juvenile dispersal following larval metamorphosis.

B. MATERIALS AND METHODS

1. Species considered

Prosobranchs of the marine genus *Lacuna* represent a group of small (adult size: 3-12 mm shell length) herbivores abundant on seaweeds in various areas of the North Atlantic and Pacific coasts. They are among the most abundant grazers found in both intertidal and subtidal seaweed communities (Smith, 1973; Fralick *et al*., 1974; Smith *et al*., 1985; Johnson and Mann 1986; Martel, unpublished). The genus exhibits wide variations in shell shape and colour morphs, making species differentiation confusing, particularly among small juveniles (Kozloff, 1987; Martel, unpublished). Shell coloration and shape, radular characteristics and reproductive ecology have been used to differentiate the *Lacuna* species (Johnson, 1960; Warburton, 1979; Langan 1984). In the San Juan Islands (Washington, USA), Strait of Juan de Fuca and Vancouver Island (B.C.)., at least two species are commonly found: *L. variegata* and *L. vincta* (Kozloff, 1983; Martel, unpublished). In the present study, newly-metamorphosed individuals raised in the laboratory have shown that *L. vincta*, the larger of the two, is the dominant species that settles in the canopies of *Macrocystis integrifolia* and *Nereocystis luetkeana* beds.

2. Spawning cycle (oviposition)

This study was conducted in Barkley Sound, on the west coast of Vancouver Island, in the vicinity of the Bamfield

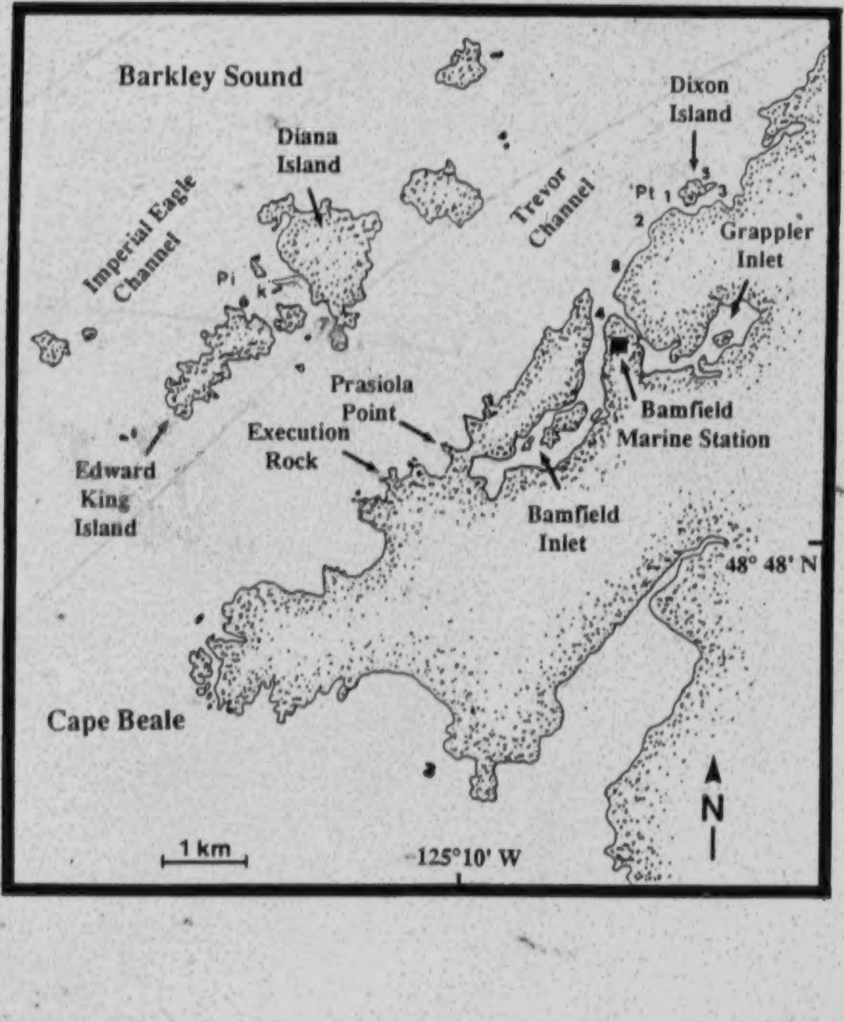
Marine Station (48° 50′N, 125° 08′W) (Fig. 2.1). To determine periods of oviposition for *Lacuna vincta* and *L. variegata*, I monitored abundance of egg masses on intertidal seaweeds from April 1987 through November 1988. I sampled from three to six quadrats (0.1 m^2 i.e. 31.7 cm X 31.7 cm) of different intertidal seaweed species (in Grappler Inlet: *Fucus disticus* and *Zostera marina*; at Prasiola Point: *Hedophyllum sessile*; at Execution Rock: *Iridaea cordata*) (see Fig. 2.1) at 4 to 6-week intervals. Distinction between egg masses of the two species was made using size and shape characteristics. Field and laboratory observations of recently deposited egg masses revealed that those of *L. vincta* were larger in diameter (4-6 mm) than those of *L. variegata* and had a definite doughnut shape, with a characteristic hole in the middle. The distinction between spawns was also facilitated by the tendency of each species to be more abundant and to deposit more egg masses onto different species of seaweeds (e.g.: *L. vincta* on *H. sessile*, *L. variegata* on *I. cordata*). Colour of egg masses was not a reliable characteristic since it varies with the animal's diet (Martel, unpublished; see Chapter IV).

3. Abundance and growth of larvae in the plankton

I quantified the abundance and growth of *Lacuna* spp. larvae in the field by taking plankton tows every 2-4 weeks, from February 1987 through September 1988. Plankton tows during May of 1989 enabled comparisons of timing of peak

Figure 2.1. Field sites in southeast Barkley Sound, west coast of Vancouver Island, British Columbia, Canada. Pt and Pi indicate location of plankton sampling sites in Trevor (Pt) and Imperial Eagle (Pi) Channels. Numbers indicate sampling locations for *Macrocystis integrifolia* (1, 3, 4, 5, 6, 7, 8) and *Nereocystis luetkeana* (2) beds. (k) indicates location of kelp farm on north side of Edward King Island. Bottom figure is enlargement of area indicated in top figure. Modified from Roland (1980).

Vancouver Island
Pacific Ocean


Barkley Sound
Diana Island
Imperial Eagle Channel
Trevor Channel
Dixon Island
Pt
1
2
3
5
8
4
Grappler Inlet
Pi
k
6
7
Prasiola Point
Execution Rock
Bamfield Marine Station
Edward King Island
Bamfield Inlet
48° 48' N
Cape Beale
N
1 km
125°10' W

larval settlement with the preceding years. Samples were taken at two sites: the first was relatively protected, in Trevor Channel on the south-west side of Dixon Island, and the second was north of Edward King Island in the more exposed waters of Imperial Eagle Channel (Fig. 2.1; sites Pt and Pi, respectively). Zooplankton tows were taken with a 125 µm mesh, 0.5 m diameter plankton net. In order to standardize samples, tows were always taken 2 to 3 hours before the daytime high tide, for a period of five minutes, moving at approximately 1 m / s (2 knots). The net was kept at a constant depth of 2-3 m using a buoy and a 1 kg lead weight. The volume of water filtered was measured using an "Oceanic" flow meter, which enabled estimation of larval density. Plankton samples were sorted upon arrival in the laboratory and Lacuna larvae were differentiated from other larval genera using characteristics including protoconch (larval shell) shape, texture of the shell surface (microvillosities on the first few coils), and velum shape and pigmentation. Larvae raised in the laboratory were initially used for comparison and verification purposes. Since it was not possible to identify the different species of Lacuna larvae with confidence, they were pooled as "Lacuna spp.". The veligers of gastropod species other than Lacuna spp. were pooled as "veliger spp.".

Since it was not always possible to collect plankton samples from Dixon Island and Edward King Island on the same day, I used monthly averages for comparisons of seasonal trends in abundance of Lacuna spp. larvae between the two sites. Samples from Edward King Island were unavailable during March, October and December of 1987; therefore these three months were not considered when comparing trends in larval abundance between the two sites for the 1987/1988 period.

I studied the growth of Lacuna veligers in the plankton from samples taken in Trevor Channel (Fig. 2.1, site Pt) throughout the winter and spring of 1988, as well as during May of 1989. Lacuna larvae were counted and the length of the protoconch was measured under a dissecting microscope (greatest length of larval shell; dorsal side up, ±10 µm). These measurements allowed me to study cohorts of Lacuna spp. larvae in the plankton.

4. Larval settlement, density and size-frequency distributions of juveniles in kelp canopies

I monitored settlement -- the term settlement includes the exploratory behaviour and metamorphosis of the larvae on the substratum -- of Lacuna vincta by monthly sampling of Macrocystis integrifolia and Nereocystis luetkeana blades from beds south-west of Dixon Island (Fig. 2.1, beds #1 and #2, respectively) between February 1987 and September 1988. Random samples of blades near the surface of kelp canopies were taken during daytime low tide. In Barkley Sound, Macrocystis beds often form long bands running along the shore and are usually delimited on the inshore side by the

0 m tide level, and the offshore side by the -4 m tide level (Wheeler and Druehl, 1986). At low tide, most of the blades float near the surface, except for those senescing near the holdfast. Thus, taking samples during low tides, at various distances from the frond meristem, ensured collection of both young and mature blades. Each sample of Macrocystis and Nereocystis consisted of 7-15 blades collected from an area of 2-4 m in radius. Blades were carefully taken out of the water, placed into labelled plastic bags and brought to the laboratory (from 3 to 6 samples; approx. wet weight: 400-900 g each). Comparisons between the numbers of juveniles on blades sampled during SCUBA diving indicated that newly-metamorphosed juveniles were not dislodged when sampled from the surface. Washing the blades in warm fresh water effectively removed all non-sessile invertebrates. Following their removal, I collected juvenile L. vincta by passing samples through 125 µm Nitex filters. Snails were then counted and measured (dorsal view) under a dissecting microscope. Regression equations relating area to dry weight of sampled blades were used to calculate the total blade area of each sample and the density of newly-metamorphosed juveniles in the canopy. To compensate for seasonal variations in the dry weight proportion of blades, I calculated regression equations for various periods of the year.

5. Evidence of juvenile drifting in kelp beds

a. Transplant experiments

Transplant experiments were undertaken to test the hypothesis that juvenile Lacuna vincta can voluntarily drop off. A total of 32 juveniles, between two and three mm shell length, were each placed onto a Macrocystis blade. Adhesion and tenacity of juveniles were tested by rapidly moving the blade back and forth in a large pan filled with seawater and were again verified using the same method at the time the blades were transplanted into the kelp bed. Snails that were dislodged during this procedure were replaced with other individuals and their adhesion tested. To eliminate potential predation, treatment blades were put into cages (30 x 80 x 80 cm) wrapped with seine net (1 and 7 cm mesh size). Two such treatment cages, containing three Macrocystis blades each, were placed at the outer edge of a kelp bed at Dixon Island on 2 June 1987, 1-1.5 m below the surface (water depth at site: 6-8 m). This corresponded to the period when most juveniles had just disappeared from natural kelp bed canopies following the spring recruitment. The Macrocystis bed situated on the east side of Dixon Island was used for the transplant experiments and was protected from wave action (Fig. 2.1, bed #3). Control blades (n = 6) were not put into cages (a total of 384 snails for treatment and control blades). At the end of three days, blades were collected and placed in individual plastic bags for later examination in the laboratory.

b. Off-bottom collectors

Off-bottom collectors were employed to demonstrate that juveniles drift in the water column. Ten collectors made of 2.5 or 0.8 cm mesh galvanized hardware cloth (12 X 20 X 35 cm) were placed at the outer edge of *the Macrocystis* beds at three different sites: in Bamfield Inlet, at the north sides of Dixon and Edward King Islands (Fig. 2.1, beds #4, 5, 6). Each collector was maintained in the water column (1-3 m below the surface; 4-12 m depth) by means of an anchor line and small buoys. Single precleaned *Macrocystis* blades were attached by both extremities in the center of the cage. From a small boat, collectors were lifted and washed individually in a pan of freshwater at 24 or 48 hour intervals to remove invertebrates that had attached the kelp in the collector. Juvenile *Lacuna vincta* were then gathered by filtration and taken to the laboratory for measurements.

6. Vertical size distribution of *Lacuna vincta* along *Macrocystis* fronds

The size distribution of *Lacuna vincta* along a vertical gradient, over wild *Macrocystis* fronds was determined by sampling complete fronds in the *Macrocystis* beds at Diana and Dixon Islands (Fig. 2.1, beds #7 and 2) during the fall recruitment of 1988 and that of the spring of 1989. *Macrocystis* fronds were cut at the holdfast during the daytime low tide, using a V-shaped knife attached to a 4 m stick.

In the laboratory, fronds were suspended horizontally and cut, beginning at the tip, into 0.5 or 1 m sections. To remove the snails, blades from each section were washed in a large freshwater filled pan. The snails from each blade were placed into small vials to be counted and measured later with the aid of a dissecting microscope.

7. Canopy versus undercanopy recruitment

To compare intensity of recruitment and size-frequency distributions of Lacuna vincta among seaweeds of the canopy (blades) and the undercanopy (other algae growing on the kelp forest floor), samples (0.1 m^2 quadrats) of benthic algae were randomly taken along transects perpendicular to the shore at the Triangle Mark and Dixon Island Macrocystis bed (depth: 2-6 m) (Fig. 2.1, bed #1 and 8). The undercanopy seaweed community was represented by numerous species which were often patchy in distribution and included many red (Rhodymenia spp., Gigartina spp.) and brown (Dictyota binghamiae and Desmerastia sp.) algae. Samples were taken using a modified air-lift apparatus with interchangeable cassette containers made of 4 inch PVC pipes with 600 µm mesh Nitex windows. In order to compare the recruitment of L. vincta in the overlying canopy, the undercanopy was studied using the method described earlier (section 4).

8. Fish predation pressure in the field

Predation on Lacuna vincta in the field was studied by analyzing gut contents of the perch (embiotocid) Rhacochilus vacca. The fish were taken with a rod spear gun while SCUBA diving in the Macrocystis bed at Dixon Island (Fig. 2.1, bed #1) during September of 1988. Shelled-prey were identified to genus under the dissecting microscope by examining valve fragments and hinges (bivalves), shell apices, fragments of body whorls as well as shape and colour of opercula (gastropods).

9. Laboratory experiments on fish predation

Laboratory experiments on fish predation were conducted in a large display tank (150 cm long, 80 cm wide, 100 cm deep) containing one adult Rhacochilus vacca and three adult Embiotoca lateralis, sections of Macrocystis fronds and a substratum of pebbles and gravel. To test the effect of snail size and blade trough depth on predation rate, snails of four size classes were used: 1.2-1.5, 1.6-1.9, 2.0-3.0 and 4.0-5.1 mm shell length. Mature Macrocystis blades with deep troughs as well as young blades with shallow troughs were suspended side by side in the tank. For each of six trials, seven snails of each size class (a total of 28 snails per trial per blade) were lightly glued (Insta Glue) onto the blade to prevent them from dropping off (but so as not to interfere with the fishes' ability to eat them). The experiments lasted 30 minutes, after which time uneaten individuals of each size class were counted.

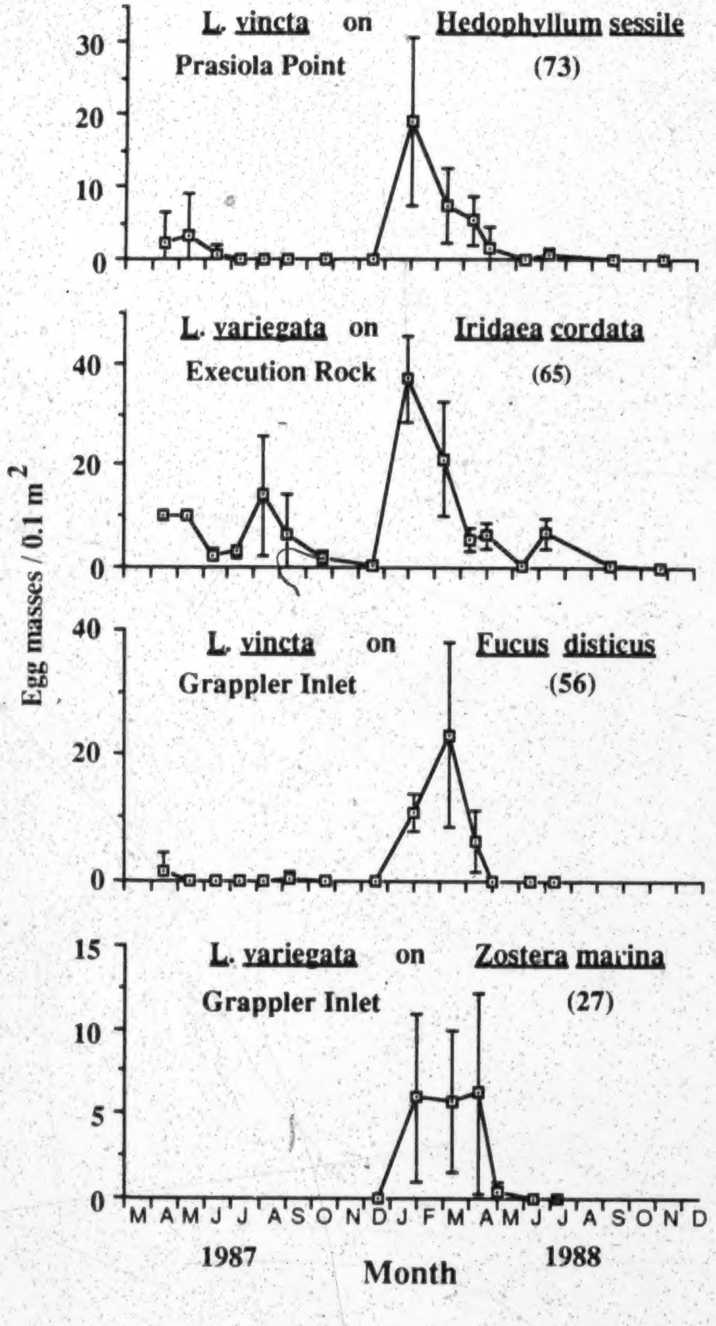
For ANOVA (One-way, Two-way and Kruskal-Wallis) and Kendall's rank correlation tests, I followed methods outlined by Sokal and Rohlf (1981).

C. RESULTS

1. Oviposition of Lacuna vincta and L. variegata

During spawning periods, Lacuna egg masses were abundant on various seaweed species of the low intertidal, but were rare in kelp canopies. Estimates of egg mass densities on intertidal seaweeds from various sites revealed that the reproductive cycle of L. vincta and L. variegata followed an annual pattern and provided evidence of a long breeding period (Fig. 2.2). Egg masses were virtually absent from all sites during mid-December of 1987. By January of 1988, spawning had begun and high densities of egg masses were observed. A synchronous spawning peak occurred during mid-winter. At Prasiola Point, mean density of L. vincta egg masses on the brown alga Hedophyllum sessile passed from near zero values during December to 19.20 egg masses / 0.1 m^2 during late January (Kruskal-Wallis, $H = 49.22$, $p < 0.001$) (Fig. 2.2). Similar increases occurred on Fucus disticus ($H = 49.21$, $p < 0.001$) and Zostera marina in Grappler Inlet ($H = 22.58$, $p < 0.001$). Egg masses of L. vincta decreased in number during the spring, becoming rare through the summer and fall. In addition to their abundance during the intense winter spawning period, egg masses of L. variegata on Iridaea

Figure 2.2. Seasonal variations in density of egg masses of *Lacuna vincta* and *L. variegata* on four species of intertidal algae from three locations in 1987 and 1988. Values shown are means, error bars represent ± SD. Number below algal species name indicates number of quadrats.


L. vincta on Hedophyllum sessile
Prasiola Point
(73)
L. variegata on Iridaea cordata
Execution Rock
(65)
L. vincta on Fucus disticus
Grappler Inlet
(56)
L. variegata on Zostera marina
Grappler Inlet
(27)
Egg masses / 0.1 m^2
0
10
20
30
40
5
15
M A M J J A S O N D J F M A M J J A S O N D
1987
1988
Month

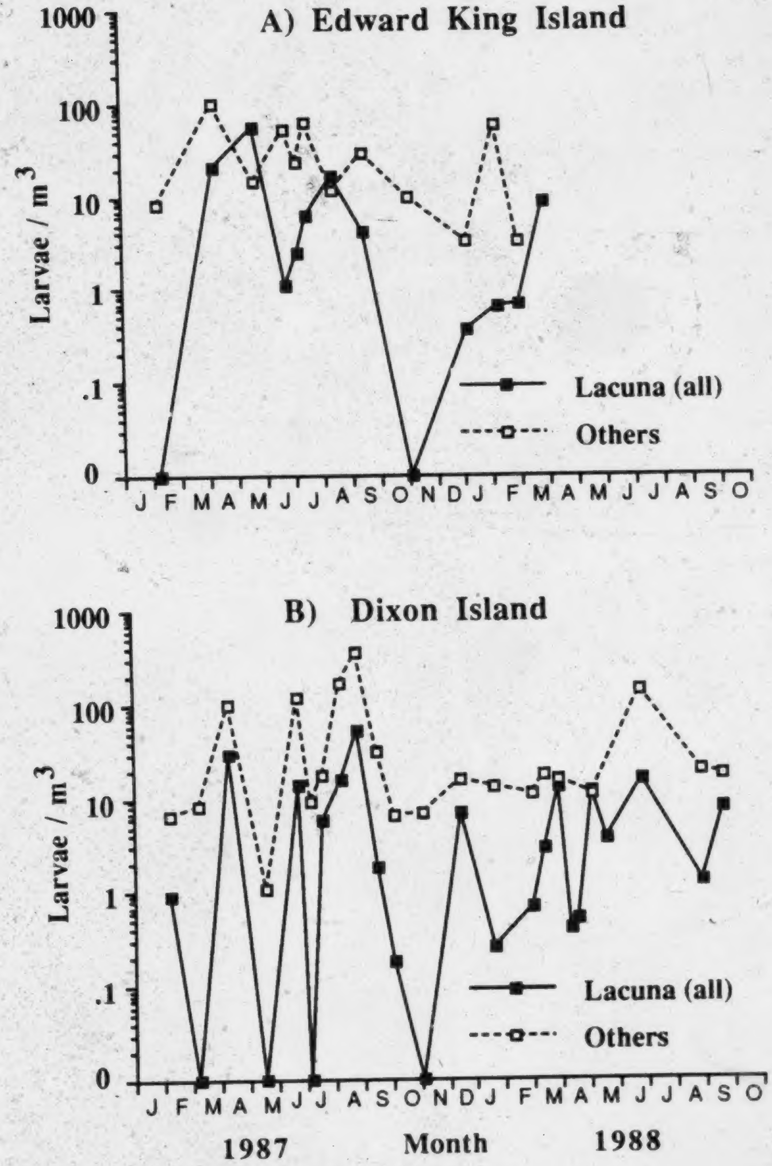
cordata were again common during mid-summer, but this time at lower densities (Fig. 2.2). For both species, however, egg masses could be found at almost any time of the year. Observations made in different areas, including the San Juan Islands and southern Vancouver Island, also showed evidence of an intensive spawning period during the winter.

Laboratory observations indicated that a time period of 2.5-3.5 weeks was required for the embryonic development (from oviposition to hatching of the planktotrophic larvae) (8-11° C). Judging from the observed timing of spawning, and the known intracapsular development time, a cohort of young larvae was expected and was found in the plankton during the month of February.

2. Abundance of planktonic Lacuna larvae in Barkley Sound

Lacuna spp. larvae (all sizes) were identified through most of the year in both near and offshore plankton samples as predicted from the essentially year-round presence of egg masses of both species (Fig. 2.3 A, B). At Edward King Island, maximum densities (all sizes) were recorded during spring and late summer (Fig. 2.3 A). Fluctuations in larval density were greater at the nearshore than at the offshore site (Fig. 2.3 A, B). Larval abundance (all sizes) at the two sites, however, followed a similar pattern from July 1987 to March 1988 (comparison between monthly averages; Kendall's rank correlation, tau = 0.8095, $p < 0.05$). Data from plankton tows also indicated that, particularly during the

Figure 2.3. Seasonal abundances of Lacuna spp. larvae (all sizes) (solid line) and of other gastropod veligers (dashed line) at 2 sampling sites in 1987 and 1988. A) North of Edward King Island, in Imperial Eagle Channel. B) Southwest of Dixon Island, in Trevor Channel.


A) Edward King Island
1000
100
10
1
.1
0
Larvae / m^3
Lacuna (all)
Others
J F M A M J J A S O N D J F M A M J J A S O
B) Dixon Island
1000
100
10
1
.1
0
Larvae / m^3
Lacuna (all)
Others
J F M A M J J A S O N D J F M A M J J A S O
1987
Month
1988

spring, Lacuna spp. larvae are an important component of the planktonic veliger population. Densities of the Lacuna spp. larvae alone were sometimes almost as high as that of all other veligers pooled together (Fig. 2.3 A).

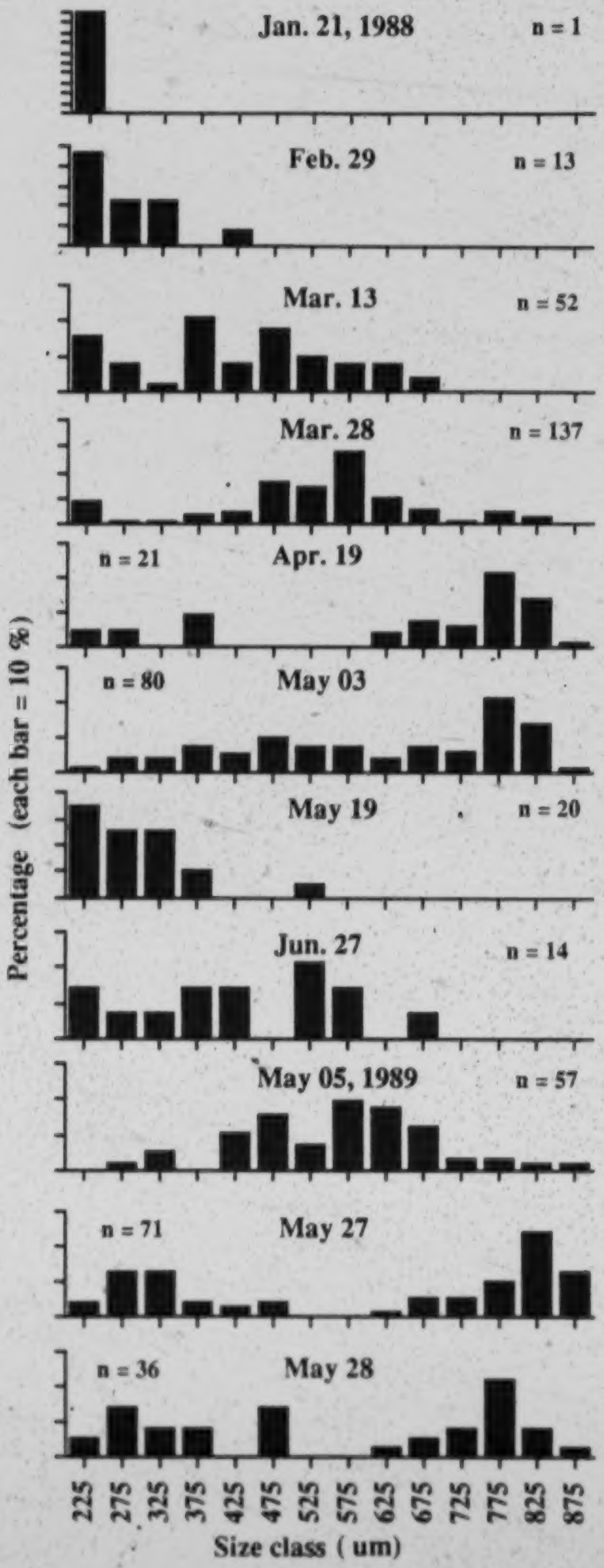
3. Larval growth in the plankton, abundance of advanced larvae and recruitment rate in kelp bed canopies

Measurements of the length of the larval shell of Lacuna spp. larvae from spring samples (1988/1989) at Dixon Island, have permitted an estimation of the duration of the planktonic period and the forecasting of the timing and rate of recruitment during the spring (Fig. 2.4). A cohort represented by recently-hatched larvae with a protoconch length of 225-325 µm (hatching occurred at 195-210 µm) can be followed from late January/mid-February to mid-April/early May (Fig. 2.4). These results revealed that planktonic larval development lasts between seven and nine weeks in Barkley Sound. During this period, the planktotrophic veligers grow considerably as shell length increases from 195-210 µm (hatching) to 775-875 µm.

In late spring/early summer, the occurrence of a second cohort of young Lacuna spp. veligers is suggested in the samples of May 19/June 27, 1988 (Fig. 2.4).

Trends in the abundance of advanced larvae (500-875 µm) between the offshore (Edward King Island) and the nearshore (Dixon Island) sites were similar from February of 1987 to March of 1988 (Kendall's rank correlation test; comparison

Figure 2.4. Size-frequency distributions of Lacuna spp. larvae sampled southwest of Dixon Island, in Trevor Channel, between January 21 and June 27, 1988, and between May 03 and May 28, 1989. Number beside date indicates number of veligers.


Jan. 21, 1988
n = 1
Feb. 29
n = 13
Mar. 13
n = 52
Mar. 28
n = 137
n = 21
Apr. 19
n = 80
May 03
May 19
n = 20
Jun. 27
n = 14
May 05, 1989
n = 57
n = 71
May 27
n = 36
May 28
Percentage (each bar = 10 %)
225
275
325
375
425
475
525
575
625
675
725
775
825
875
Size class (um)

between monthly averages; tau = 0.6873, $p < 0.01$) (Fig. 2.5). Furthermore, the abundance of advanced Lacuna spp. larvae was indicative of major settlement periods, with a peak during the spring (April) and another, of lower intensity, during late summer-fall during the three years of this study (compare Figs. 2.5 and 2.6). During April-early May, a significant proportion of the larvae was advanced and had attained metamorphic competence. Growth rate of the larvae deduced from the cohorts, and the size at metamorphosis indicated that an intense period of settlement was imminent at the end of March, 1988 (Fig. 2.4). Indeed, a strong pulse of spring settlement occurred during the weeks following (Figs. 2.5, 2.6). At the beginning of this intense settlement period, advanced larvae of 775 µm were common in the plankton (Figs. 2.4, 2.5). Settlement of these competent larvae was confirmed through the presence and the size distribution of newly-metamorphosed juveniles in the Macrocystis canopy on April 5, 1988, with a distinct mode at 0.775 mm shell length (Fig. 2.7). Thus, the study of larval growth in the plankton allowed the prediction of the timing and rate of recruitment of L. vincta.

Inspection of blades for newly-recruited juveniles is simplified because of the homogeneity and transparency of kelp blades when using natural or artificial backlighting. Lacuna vincta larvae settling and metamorphosing in kelp bed canopies can also be readily detected because of their large size at settlement (675-875 µm) -- the time interval between

Figure 2.5. Seasonal abundances of advanced (> 500 µm) *Lacuna* spp. larvae at 2 sampling sites. A) North of Edward King Island, in Imperial Eagle Channel. B) Southwest of Dixon Island, in Trevor Channel.

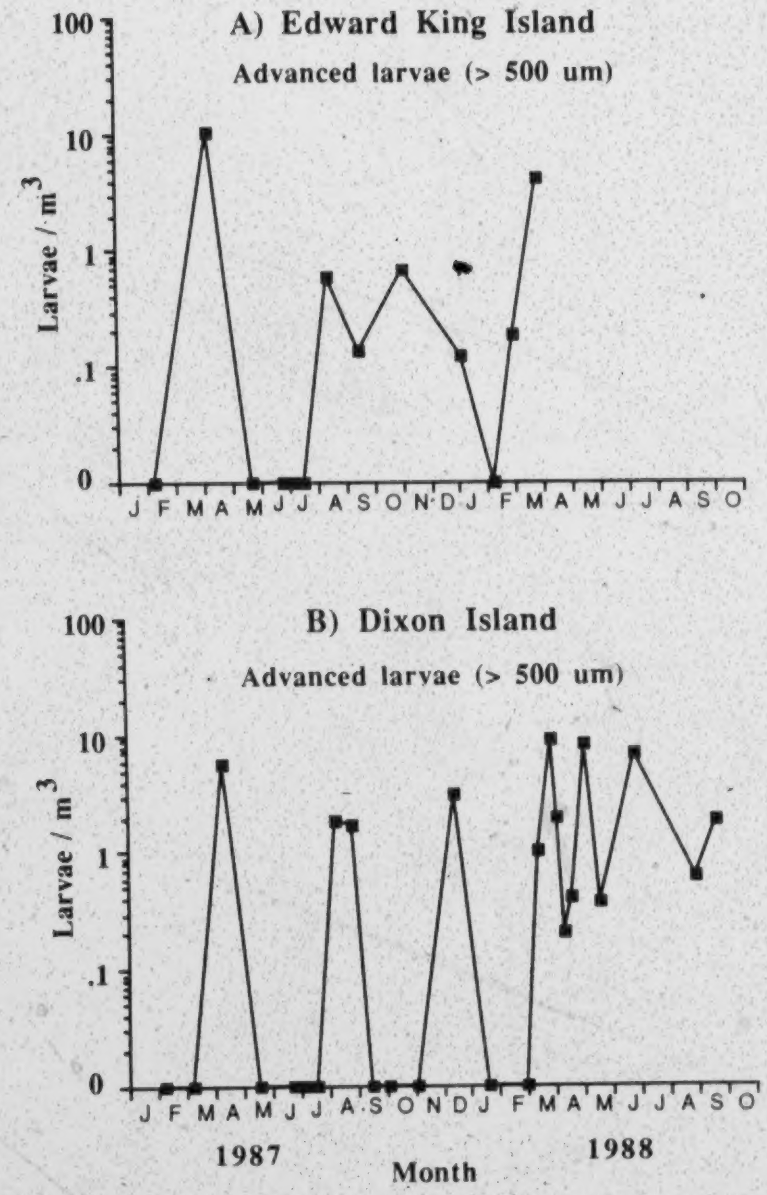

A) Edward King Island
Advanced larvae (> 500 um)
Larvae / m^3
100
10
1
.1
0
J F M A M J J A S O N D J F M A M J J A S O
B) Dixon Island
Advanced larvae (> 500 um)
Larvae / m^3
100
10
1
.1
0
J F M A M J J A S O N D J F M A M J J A S O
1987
1988
Month

Figure 2.6. Seasonal abundances of *Lacuna vincta* on kelp bed canopies (blades) southwest of Dixon Island. A) *Macrocystis integrifolia*, B) *Nereocystis luetkenea*. Points indicate mean densities. Number below genus name indicates number of samples. Error bars represent ± SD.

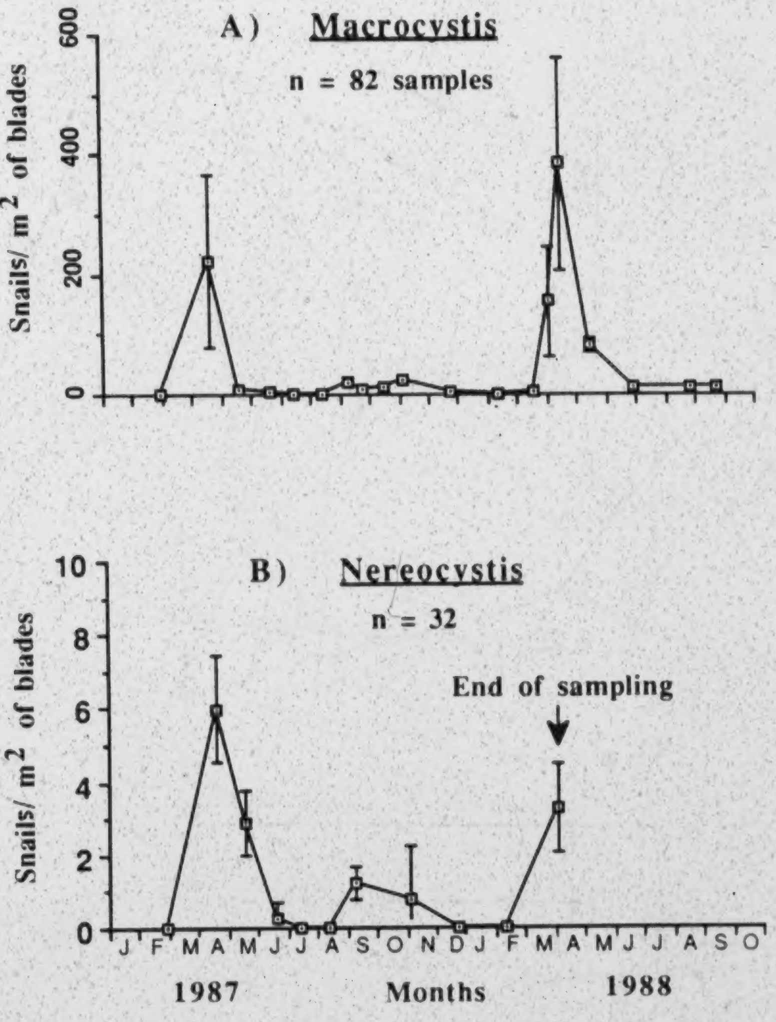
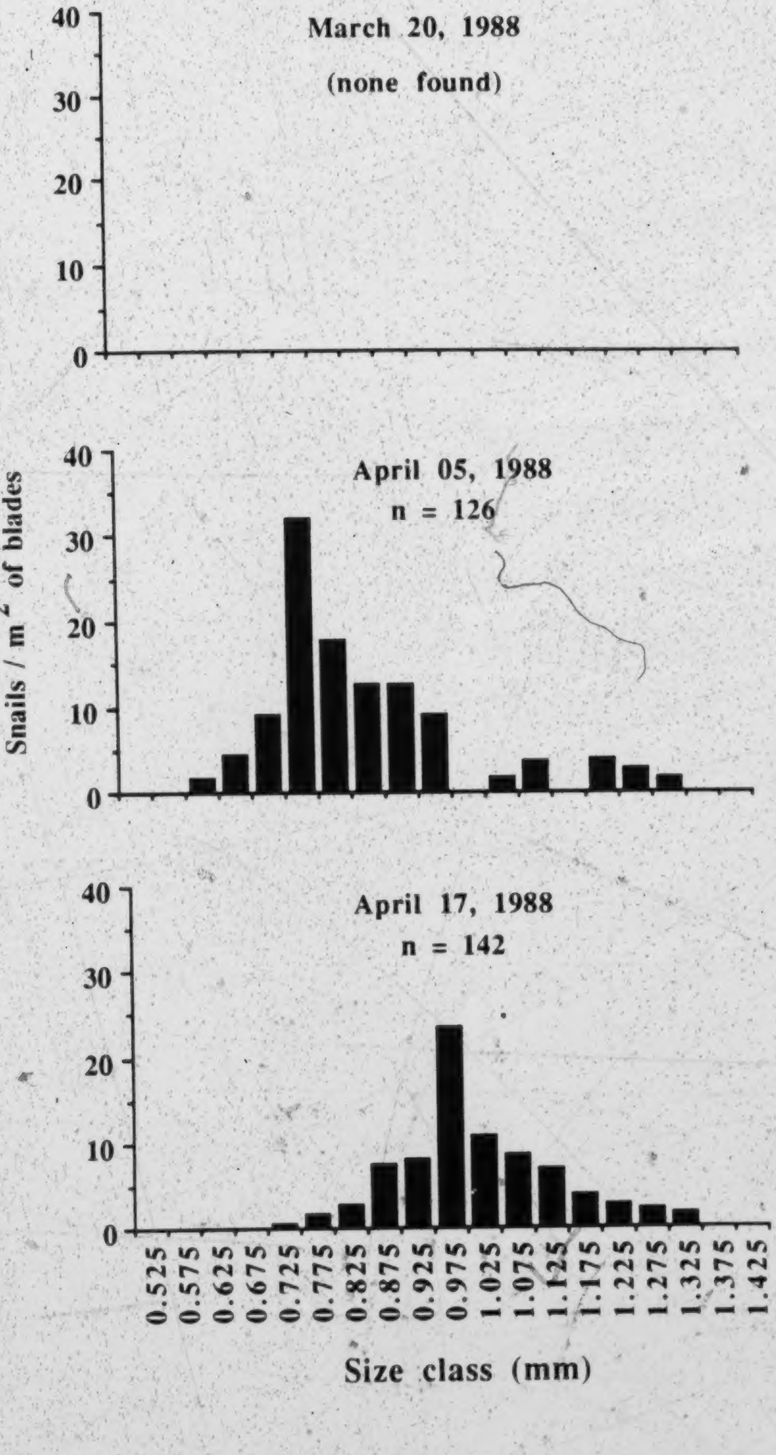

A) Macrocystis
n = 82 samples
Snails/ m^2 of blades
600
400
200
0
B) Nereocystis
n = 32
End of sampling
Snails/ m^2 of blades
10
8
6
4
2
0
J F M A M J J A S O N D J F M A M J J A S O
1987
Months
1988

Figure 2.7. Size distributions of juvenile Lacuna vincta in the canopy of Macrocystis integrifolia beds, southwest of Dixon Island, before (A: March 20) and during (B, C: April 05 and 17) spring settlement. Histograms show mean numbers of newly-metamorphosed juveniles of each size class. Number below the date indicates number of samples. Note the mode at 0.775 mm observed in the sample of April 05, 1988.


March 20, 1988
(none found)
April 05, 1988
n = 126
April 17, 1988
n = 142
Snails / m2 of blades
0
10
20
30
40
0.525
0.575
0.625
0.675
0.725
0.775
0.825
0.875
0.925
0.975
1.025
1.075
1.125
1.175
1.225
1.275
1.325
1.375
1.425
Size class (mm)

metamorphosis and recruitment is nil. Hence, I consider recruitment rate to follow a trend similar to that of settlement rate.

The abundance of newly-metamorphosed juvenile Lacuna vincta in the canopy coincided with the pattern of abundance of advanced larvae (Figs. 2.5, 2.6 and 2.7). For bimonthly comparisons (averages for January-February, March-April, etc.) patterns of abundance of advanced larvae at Dixon Island and that of the newly-metamorphosed juveniles on Macrocystis followed similar trends (Kendall's rank correlation, tau = 0.7192, $p < 0.01$). The same is true when comparing the pattern of abundance of advanced larvae observed at Edward King Island (tau = 0.7407, $p < 0.05$).

During peak settlement, numbers of newly-metamorphosed juveniles in the Macrocystis canopy were high and individuals on the blades could even be seen from the water surface. Densities as high as 565 juvenile Lacuna vincta / m^2 of Macrocystis blade have been observed (17 April 1988). From near zero values in the winter, densities increased sharply during mid-spring (Kruskal-Wallis; 1987: $H = 15.16$, $p < 0.005$; 1988: $H = 24.14$, $p < 0.001$), with averages of 221.9 and 383.9 individuals / m^2 of blades during April of 1987 and 1988, respectively (Fig. 2.6 A).

Densities of juveniles were comparatively lower during the fall recruitment period, increasing from low summer values to about 6-21 individuals / m^2 of canopy during the fall (Kruskal-Wallis, 1987: $H = 28.44$, $p < 0.001$) (Fig. 2.6).

It must, however, be noted that the total numbers and the densities of blades on the Macrocystis plants varied markedly with the seasons, being at their lowest during winter-early spring and at their highest during late summer-early fall. Therefore, to estimate population of juveniles in this habitat, or the number per m^2 of bottom, a correction factor, the "Leaf Area Index", or LAI, described by Wheeler and Druehl (1986), should be used (ratio between the number of m^2 of Macrocystis blades overlying each m^2 of bottom). During the spring, the density of juvenile Lacuna vincta per area of blades resembles that of per area of bottom, the LAI value being close to 1 (1 m^2 blade / m^2 bottom). However, an important difference between these two densities is observed during late summer-fall when the LAI can reach up to 11.9 (Wheeler & Druehl, 1986). Thus, because Macrocystis beds are much more dense in late summer-early fall (high LAI values), estimates of juvenile densities in the canopy (individuals / m^2 of blades) during that period underestimate the total number of individuals found per m^2 of Macrocystis bed habitat (Fig. 2.6 A).

Patterns of recruitment in Macrocystis and Nereocystis canopies were similar (Kendall's rank correlation test, tau = 0.7648, $p < 0.01$). Overall spring densities of juveniles on Macrocystis were, however, between 10X and 100X higher than those on Nereocystis (Figs. 2.6 A, B). Possible explanations for such drastic differences in densities between these two habitats may involve differences in blade surface structures and microhabitats used by juveniles. Nereocystis blades are uniform and entirely flat, lacking the folds and troughs utilized by the newly-metamorphosed Lacuna vincta on Macrocystis. The importance of these troughs to the juveniles was demonstrated by field observations. On May 6, 1989, at Dixon Island, 136 of 138 juveniles (98.6%) observed on Macrocystis blades were found crawling inside the troughs (G-test, G(williams) = 63.75, $p < 0.001$).

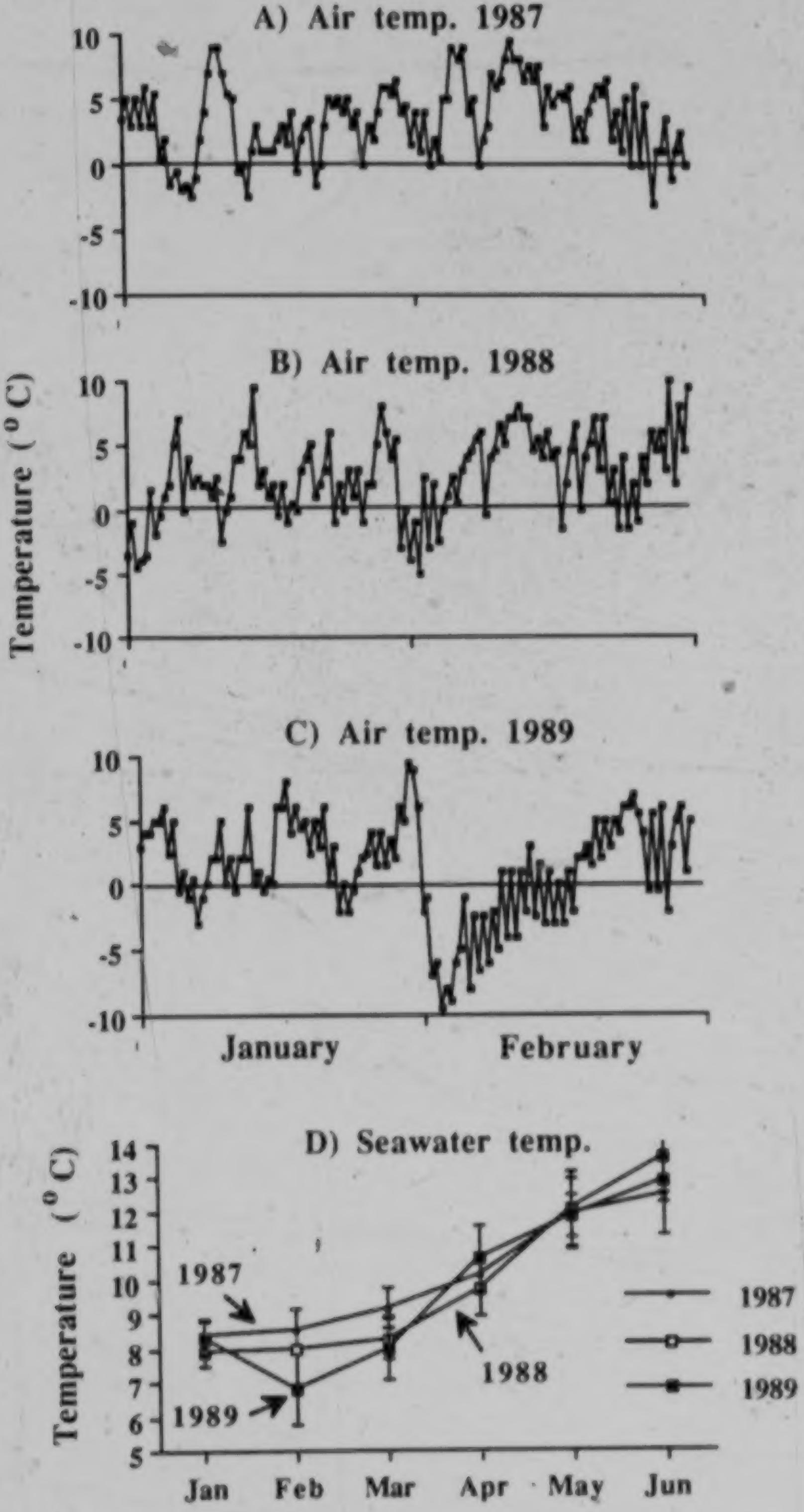
Results on abundance of advanced larvae and metamorphosed juveniles indicated annual variations in recruitment rates, with recruitment more intense during 1988 than during 1987. In Trevor Channel (Dixon Island), where plankton samples were taken over a longer period, observed abundances of advanced larvae prior to and during the spring recruitment period, were significantly higher during 1988 than during 1987 (Mann-Whitney, $Z = 2.44$, $p < 0.02$) (Fig. 2.5 B). Similarly, densities of metamorphosed juvenile Lacuna vincta in Macrocystis bed canopies for the period of April-May-June (main recruitment period) were significantly higher during 1988 than during the year before (Mann-Whitney, $Z = 2.45$, $p < 0.02$) (Fig. 2.6 A).

4. Temperature and the timing of peak recruitment

Two lines of evidence suggest that spring settlement peaked nearly a month later during the spring of 1989 than during the two preceding years. First, a cohort of larvae, with a mode at 575 µm shell length, was observed on May 5, 1989, followed three weeks later (on May 27) by the presence of a distinct cohort of advanced larvae of 825 µm shell length (Fig. 2.4). Two additional plankton samples taken on May 28 confirmed the presence of these advanced larvae in the plankton (Fig. 2.4). In 1988 similar cohorts were observed as early as March and April (Fig. 2.4). Second, during late May of 1989, intense settlement of Lacuna vincta larvae was still observed in Macrocystis beds, while at the same period during 1987 and 1988, settlement had nearly ended (Figs. 2.4, 2.5 B).

A factor potentially responsible for the late spring settlement during 1989 may be an extended period of abnormally low temperatures observed during late January-February of the same year (Fig. 2.8). The intensity and duration of the cold weather system that occurred during 1989 can be seen in Figure 2.8 C. Although the average surface seawater temperature is usually stable or slightly increasing between January and February (Fig. 2.8 D), a sharp decline occurred during that period in 1989 (monthly average for January: 8.33° C; February: 6.7° C; Mann-Whitney, $Z = 5.65$, $p < 0.001$). Seawater temperatures were also significantly lower during February of 1989 compared with 1987 and 1988 (ANOVA, $F = 38.7$, $p < 0.001$). I suggest that this unusually cold period, which occurred during Lacuna's peak spawning period, slowed intracapsular development of embryos, particularly when egg masses were exposed to sub-zero air temperatures for many consecutive days at low tide. In

Figure 2.8. Temporal variations in air and surface seawater temperatures in the vicinity of Bamfield. A, B, C) Minimal air temperatures recorded during the morning and the afternoon for each day in Grappler Inlet, during January and February of 1987, 1988, 1989. D) Monthly average surface seawater temperatures at Cape Beale, between January and June of 1987, 1988, and 1989. Values show monthly means of daily recordings. Error bars represent ± SD.


A) Air temp. 1987
B) Air temp. 1988
C) Air temp. 1989
Temperature (°C)
10
5
0
-5
-10
January
February
D) Seawater temp.
Temperature (°C)
14
13
12
11
10
9
8
7
6
5
Jan
Feb
Mar
Apr
May
Jun
1987
1988
1989

addition, it could also have reduced growth rates of larvae during the first few weeks of planktonic life. Eventually, this may have led to the late spring recruitment period observed during 1989.

5. Size-frequency distributions of Lacuna vincta in kelp canopies and dominance of juveniles

A striking feature of the size distribution of Lacuna vincta found in the kelp canopy is persistence of newly-metamorphosed juveniles throughout the year (Figs. 2.9, 2.10). Adult L. vincta and egg masses were rare in kelp bed canopies (observed during winter months -- peak spawning period -- on blades close to the bottom). Observations made during SCUBA dives suggest that adult L. vincta found on Macrocystis fronds during the winter could have crawled up from the bottom (undercanopy) during their search for egg laying sites. In contrast, I observed mainly juveniles (shell length 0.9-1.1 mm) in the kelp bed canopy, with few individuals exceeding 1.5 mm (Figs. 2.9, 2.10). There was no evidence that juveniles reached adult size in this habitat (Figs. 2.9, 2.10). Despite this fact, laboratory experiments have consistently shown that growth rates of L. vincta on Macrocystis and Nereocystis are high (see changes in size distributions of juveniles on April 5 and April 17, 1988, Figs. 2.7 and 2.10). Newly-metamorphosed individuals reared on Macrocystis can reach sexual maturity (3.5-4.5 mm) after only three months (Martel, unpublished; see Chapter IV).

Figure 2.9. Average sizes of *Lacuna vincta* found in the canopy of a *Macrocystis integrifolia* bed, at Dixon Island, in 1987 and 1988. Values show monthly means. Number above mean indicates sample size. Error bars represent ± SD.

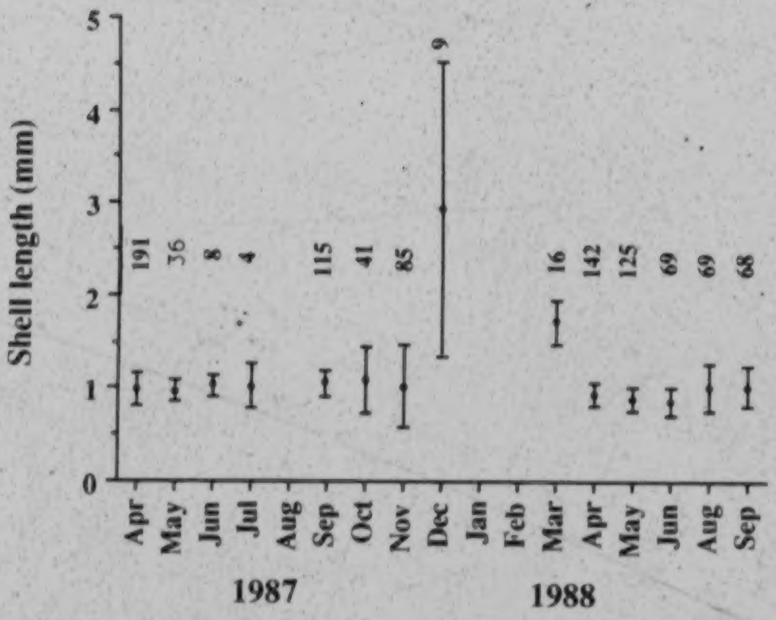
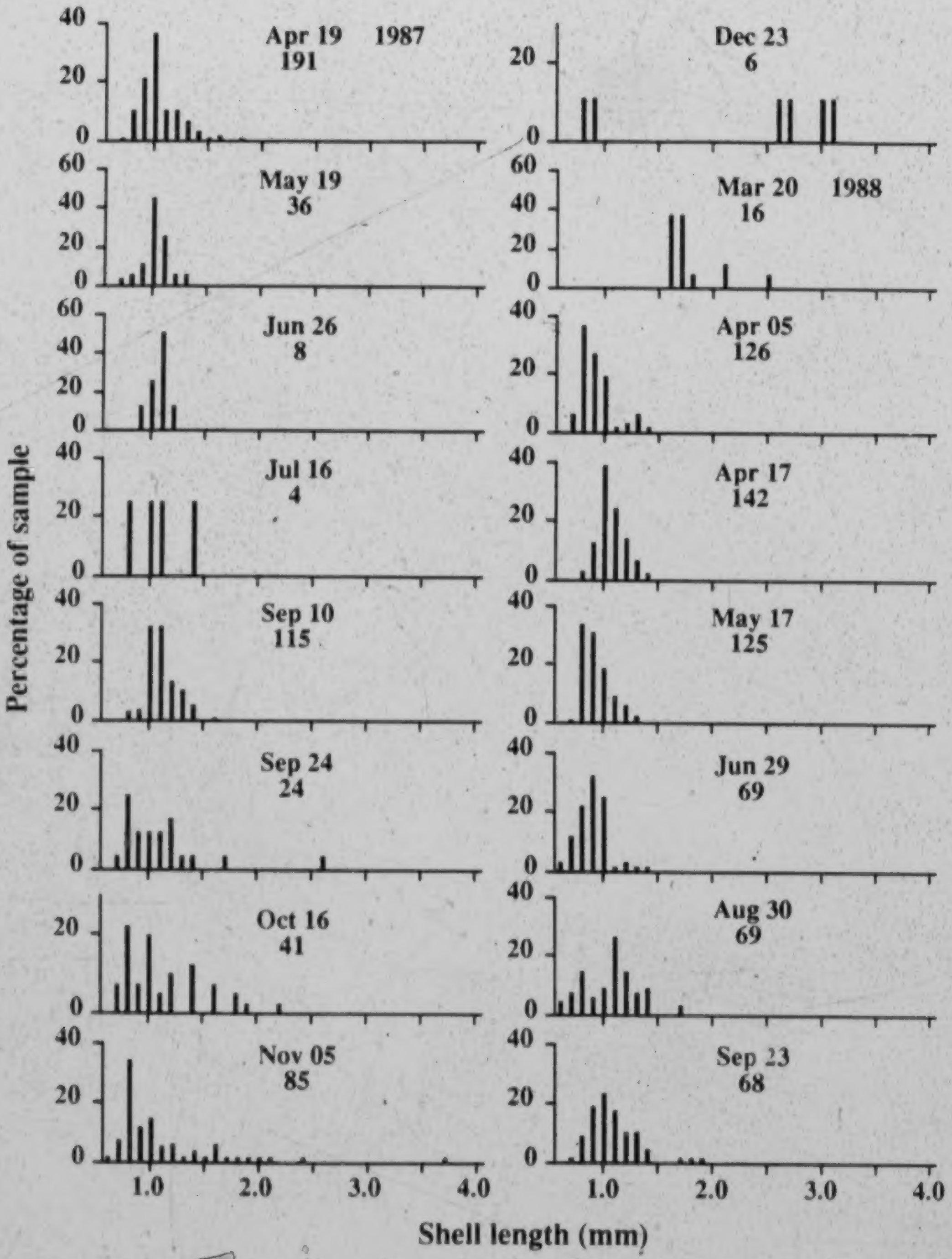

Shell length (mm)
0
1
2
3
4
5
191
36
8
4
115
41
85
9
16
142
125
69
69
68
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Aug
Sep
1987
1988

Figure 2.10. Size-frequency distributions of *Lacuna vincta* in the canopy of a *Macrocystis integrifolia* bed at Dixon Island, from April 19, 1987 to September 23, 1988. Histograms show percentage of samples for each size class. Numbers below dates indicate sample size.


Percentage of sample
Apr 19 1987
191
May 19
36
Jun 26
8
Jul 16
4
Sep 10
115
Sep 24
24
Oct 16
41
Nov 05
85
Dec 23
6
Mar 20 1988
16
Apr 05
126
Apr 17
142
May 17
125
Jun 29
69
Aug 30
69
Sep 23
68
0
20
40
60
1.0
2.0
3.0
4.0
Shell length (mm)

Moreover, densities of juveniles in the *Macrocystis* and *Nereocystis* canopies dropped rapidly soon after peak recruitment periods ended (usually < 10% of their original value within 4-6 weeks following settlement; Fig. 2.6). Consequently, these results suggest that either juveniles are subject to high mortality rates or they disperse shortly after metamorphosis.

6. Evidence of juvenile drifting in kelp beds

a. Transplant experiments

Transplant experiments indicated that juveniles on both the caged and the control blades left the substratum in equal numbers at the end of three days (Kruskal-Wallis, $p > 0.05$; Table 2.1). The pile perch, *Rhacochilus vacca*, and the striped perch, *Embiotoca lateralis*, two common embiotocid predators found in *Macrocystis* and *Nereocystis* beds in Barkley Sound, both prey heavily on shelled-invertebrates, including a wide variety of gastropods (Martel, unpublished). The transplant experiment was primarily designed to eliminate the possibility of predation by these two species. The juveniles of these ovoviviparous fishes are 6-7 cm long at birth and could not have gone through the mesh. This indicates that predation by these fish could not have accounted for the disappearance of juvenile *L. vincta* from the blades in the cages during the transplant experiment.

Table 2.1

Drop-off rates of juvenile Lacuna vincta transplanted onto Macrocystis integrifolia blades in a kelp bed at Dixon Island. N = 384 juveniles (2-3 mm shell length). 32 juveniles per blade. Control: no cage; Treatment cages with 1 cm or 7 cm mesh net. Depth: 1-1.5 m below surface; depth of kelp bed: 6-8 m.

Treatment	Number of snails					
	Beginning of experiment			72 hours later		
Snails with cage (1 cm mesh net)	32	32	32	1	0	0
Snails without cage (control)	32	32	32	0	0	0
Snails with cage (7 cm mesh net)	32	32	32	0	4	0
Snails without cage (control)	32	32	32	3	0	1

b. Off-bottom collectors

Evidence suggests that juvenile *Lacuna vincta* drop off the blades and initiate drifting excursions in the water column. Off-bottom collectors placed several meters from the offshore side of *Macrocystis* beds demonstrated the significance of drifting of juvenile *L. vincta* in the canopy (Table 2.2, Fig. 2.11). Collectors were in place for intervals of 24 or 48 hours to avoid biases resulting from the rapid growth rate of the snails. A shell length of 1 mm was set as a minimal size distinguishing a "drifting juvenile" from a newly-settled larva (0.70-0.85 mm). This likely excludes high numbers of drifting juveniles between 0.9-1.0 mm, which could represent a significant proportion of the drifters (see Table 2.2, Fig. 2.11). Drifting juveniles were found in collectors at all experimental sites on a daily basis. As many as 17 juveniles > 1 mm were found / day / collector (average of 6.75 juveniles / day / collector for the 48 hour experiment) (Table 2.2). Many of these drifters were between 1.0 and 1.6 mm, and their numbers rapidly decreased with increasing size (Fig. 2.11). The short time the collectors were left in the field (24 or 48 hours) and the high numbers of drifters found attest to the magnitude of the drifting phenomenon occurring in the vicinity of *Macrocystis* beds.

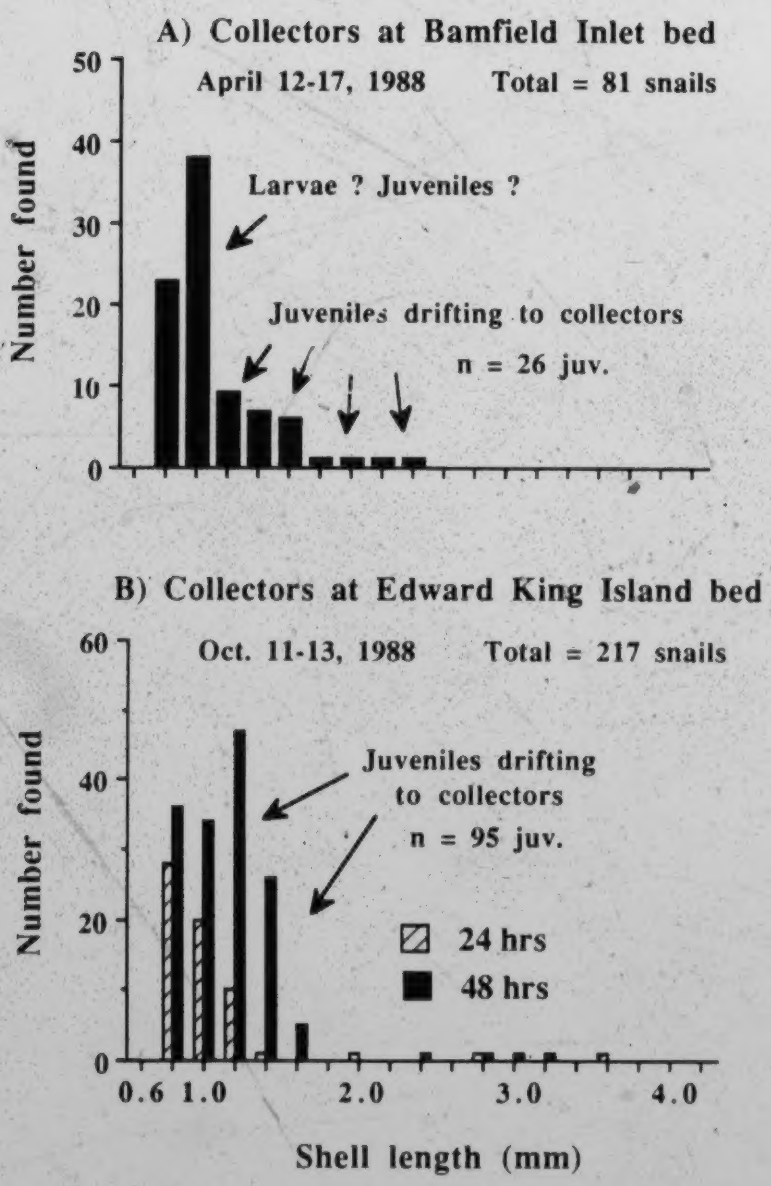
Evidence of juvenile migration was also provided by direct observations during SCUBA diving. In *Macrocystis* beds at Dixon Island, on May 28, 1987, several juvenile *Lacuna*

Table 2.2

Number of drifting juvenile Lacuna vincta trapped in off-bottom kelp collectors. Collectors were installed adjacent to the the canopy of a Macrocystis integrifolia bed at Edward King Island, on October 11-13 1988. They were left for 24 or 48 hours periods.
Depth: 1-3 m below surface; depth of kelp bed: 4-12 m.
The conservative limit of 1 mm has been used to categorize individuals arriving at the juvenile stage. Snails smaller or equal to 1 mm may have arrived as larvae.

	24 hours		48 hours	
Collector #	Juveniles > 1 mm	Juv-larv.? < 1 mm	Juveniles > 1 mm	Juv-larv.? < 1 mm
1	1	1	7	6
2	0	2	2	0
3	0	2	9	8
4	1	1	15	6
5	3	3	5	5
6	1	5	2	2
7	2	3	10	10
8	1	2	1	1
9	1	2	4	1
10	1	6	2	10
11	0	5	7	6
12	1	5	17	19
13	1	2		
14	1	9		
Avg.(ind./coll)	1	3.43	6.75	6.17
s.d.	0.78	2.78	5.22	5.29
Total no. ind.	14	48	81	74

Figure 2.11. Size distribution of Lacuna spp. found in off-bottom kelp collectors placed on the offshore side of Macrocystis integrifolia beds. A) Collectors placed at the bed in Bamfield Inlet (April 12-17, 1988) (left for 24 hour periods). B) Collectors placed at the bed at Edward King Island (October 12-14, 1988); left for 24 and 48 hour periods). Histograms show numbers of individuals of each size class trapped in collectors. As a conservative size limit, individuals > 1 mm are considered to have arrived as juveniles.


A) Collectors at Bamfield Inlet bed
April 12-17, 1988
Total = 81 snails
Larvae ? Juveniles ?
Juveniles drifting to collectors
n = 26 juv.
Number found
0
10
20
30
40
50
B) Collectors at Edward King Island bed
Oct. 11-13, 1988
Total = 217 snails
Juveniles drifting
to collectors
n = 95 juv.
▨ 24 hrs
■ 48 hrs
Number found
0
20
40
60
0.6
1.0
2.0
3.0
4.0
Shell length (mm)

vincta of 1.0-1.4 mm shell length were stimulated to drop off when the blade on which they were crawling was gently shaken. I carefully followed individuals as they left the blade and drifted slowly towards the bottom with their mucous threads. Aided by the slight tidal current (5-10 cm / s), one of these juveniles drifted 10-15 m downstream before landing and holding on to the fine branches of a red turf alga in the undercanopy where other juveniles were also found. It was estimated that this movement equalled a vertical descent of 4-5 m and took 3-4 minutes.

7. Vertical size distribution of *Lacuna vincta* along *Macrocystis* fronds

Examination of sizes of juvenile *Lacuna vincta* on the blades of the vertically-growing wild fronds from tip to holdfast, reveals significant depth-related differences in size distributions of juveniles in the kelp bed at Diana Island during periods of recruitment (One-way ANOVA; fall 1988: $p < 0.001$; spring 1989: $p < 0.05$) (Fig. 2.12). The smallest *L. vincta* were found on the upper parts of the frond, while those of intermediate sizes were found on the middle sections and the largest juveniles were observed on the blades closer to the holdfast (Fig. 2.12). A similar pattern of size distribution was observed at the more wave-exposed *Macrocystis* bed of Dixon Island during recruitment in the fall of 1988 (Fig. 2.13 A). However, for unknown reasons this vertical distribution pattern was not observed in the

Figure 2.12. Vertical size distributions of Lacuna vincta along Macrocystis integrifolia fronds at Diana Island. Histograms show the number of individuals of each size class found for each section (0.5 or 1.0 m sections) of frond, from meristem to holdfast.
A) Fronds sampled on September 14, 1988 (mature plants).
B) Fronds sampled on May 21, 1989 (young plants). Numbers at the top right indicate number of snails found in each section.

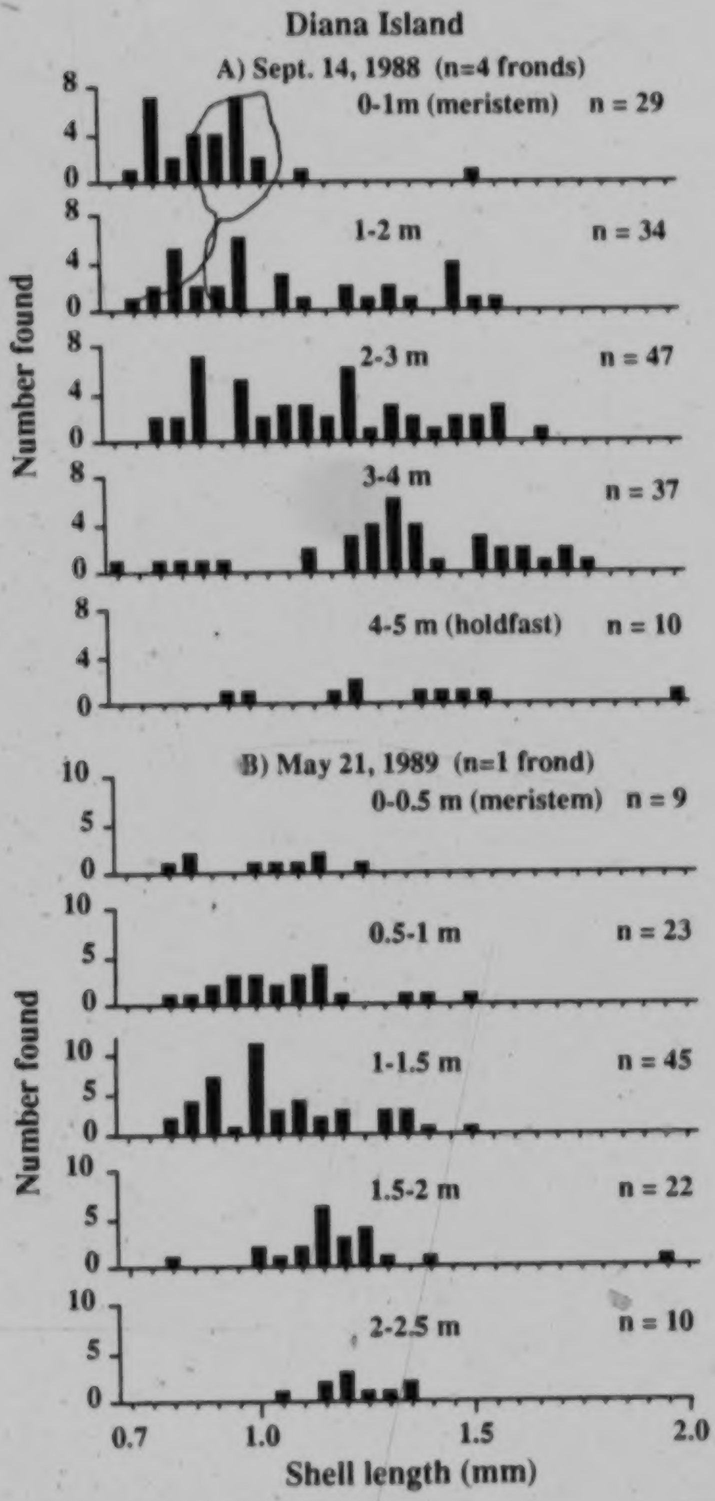
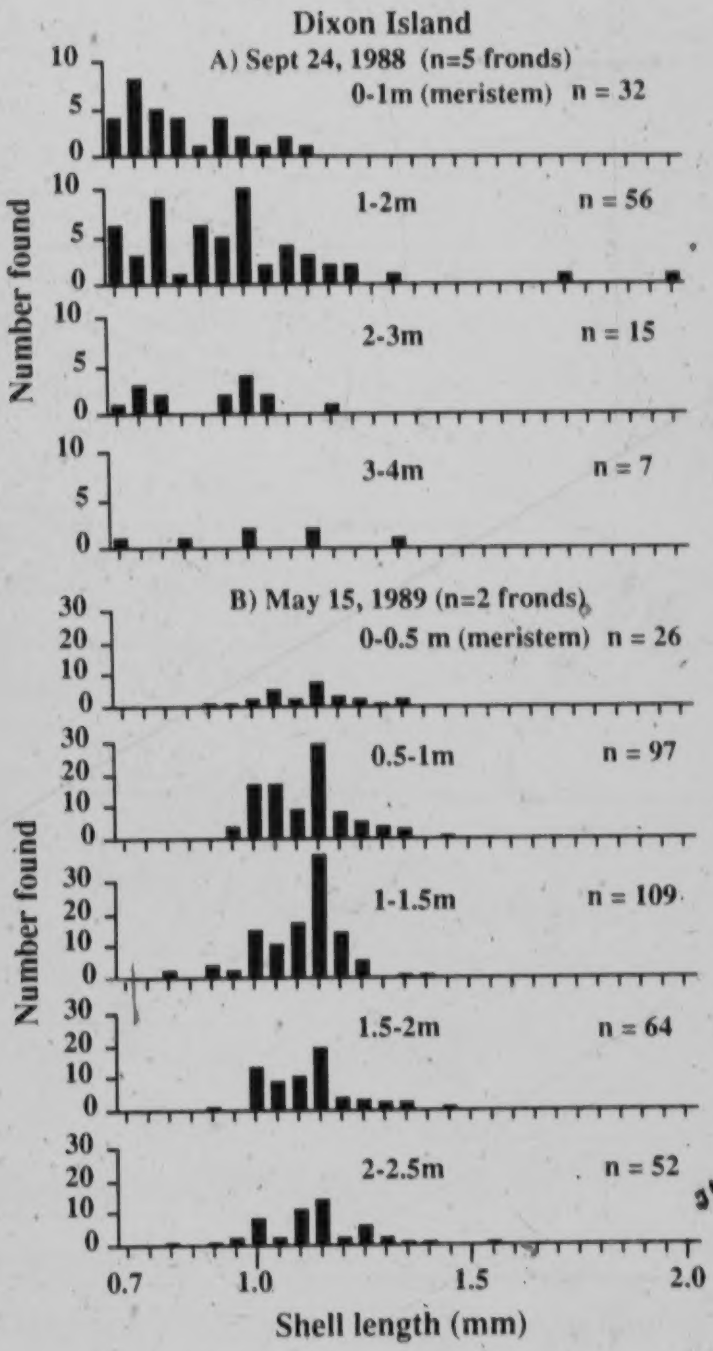

Diana Island
A) Sept. 14, 1988 (n=4 fronds)
0-1m (meristem) n = 29
1-2 m n = 34
2-3 m n = 47
3-4 m n = 37
4-5 m (holdfast) n = 10
Number found
8
4
0
B) May 21, 1989 (n=1 frond)
0-0.5 m (meristem) n = 9
0.5-1 m n = 23
1-1.5 m n = 45
1.5-2 m n = 22
2-2.5 m n = 10
Number found
10
5
0
0.7
1.0
1.5
2.0
Shell length (mm)

Figure 2.13. Vertical size distributions of _Lacuna vincta_ along _Macrocystis integrifolia_ fronds at Dixon Island. Histograms show the number of individuals of each size class found in each section (0.5 or 1.0 m sections) of frond, from meristem to the holdfast.
A) Fronds sampled on September 24, 1988; mature plants.
B) Fronds sampled on May 15, 1989; young plants. Numbers at the top right indicate number of snails found in each section.

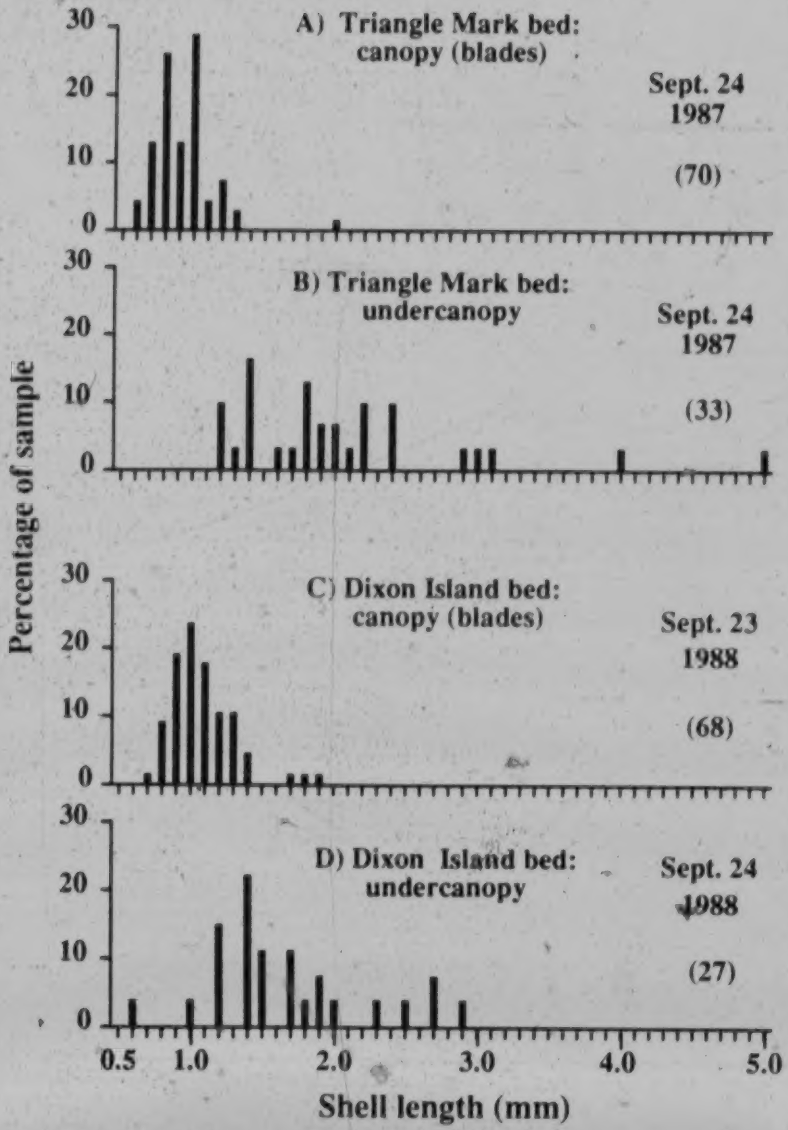

Dixon Island
A) Sept 24, 1988 (n=5 fronds)
0-1m (meristem) n = 32
1-2m n = 56
2-3m n = 15
3-4m n = 7
B) May 15, 1989 (n=2 fronds)
0-0.5 m (meristem) n = 26
0.5-1m n = 97
1-1.5m n = 109
1.5-2m n = 64
2-2.5m n = 52
Number found
Number found
0
5
10
0
10
20
30
0.7
1.0
1.5
2.0
Shell length (mm)

samples of May 1989 ($p > 0.05$) (Fig. 2.13 B).

8. Recruitment in canopy versus undercanopy

The study of the size-frequency distributions of *Lacuna vincta* during the fall recruitment period indicated that larval settlement and metamorphosis occur at a higher rate in the *Macrocystis* canopy than among the seaweeds of the undercanopy (Fig. 2.14). Sixteen air-lift quadrats (0.1 m^2) were randomly taken from the undercanopy seaweed community along four transects perpendicular to the shore at the Triangle Mark *Macrocystis* bed (Fig. 2.1, kelp bed #8). Analysis of benthos samples taken on September 24, 1987 showed the presence of large individuals, with no juveniles smaller than 1 mm (Fig. 2.14 B). On the other hand, samples taken from the overlying canopy on the same day revealed the presence of newly-metamorphosed individuals (Fig. 2.14 A). Samples taken at the Dixon Island *Macrocystis* bed on September 23, 1988, revealed similar results (Figs. 2.14 C, D). These results suggest that, compared with seaweeds of the undercanopy, the canopy of the *Macrocystis* bed may be a more important site for the settlement and metamorphosis of *L. vincta* larvae. It is possible that after a short but rapid period of growth, juveniles drop off the canopy and drift to the undercanopy and low-intertidal. A comparison between settlement rates of *L. vincta* larvae in the canopy and the undercanopy during the spring, when the total surface area of kelp is reduced, is not, however, available.

Figure 2.14. Comparison between size-frequency distributions of _Lacuna_ spp. in the canopy (mature blades; see Materials and Methods) of _Macrocystis_ _integrifolia_ beds and those in the undercanopy. Histograms show the percentage of individuals of each size class (mm). Triangle Mark bed, A) Canopy, B) Undercanopy. Dixon Island bed, C) Canopy, D) Undercanopy. Numbers in parenthesis indicate number of snails.


A) Triangle Mark bed:
canopy (blades)
Sept. 24
1987
(70)
B) Triangle Mark bed:
undercanopy
Sept. 24
1987
(33)
C) Dixon Island bed:
canopy (blades)
Sept. 23
1988
(68)
D) Dixon Island bed:
undercanopy
Sept. 24
1988
(27)
Percentage of sample
30
20
10
0
0.5
1.0
2.0
3.0
4.0
5.0
Shell length (mm)

9. Other juvenile invertebrates found in Macrocystis bed canopy

Juveniles of other non-sessile benthic marine invertebrates were observed on numerous occasions in the *Macrocystis* bed canopy. One of these is the neogastropod *Alia* (=*Mitrella*) sp. commonly found on the blades of *Macrocystis* between late spring and mid-fall. As with *Lacuna vincta*, only post-larvae and newly-metamorphosed juveniles (0.75-1.00 mm) were found in the canopy, while larger juveniles and adults were observed in the undercanopy and low intertidal seaweed community.

Interestingly, I also observed newly-settled asteroids in the *Macrocystis* canopy. Indeed, on many occasions, small juveniles of an unidentified asteroid (0.4-1.5 mm arm length) occurred on *Macrocystis* blades, with up to a dozen per blade during the summer months. The five-armed juvenile asteroids were orange or red (possibly two species), and likely belong to species with a planktotrophic larval development. On one occasion, I observed one of these juvenile asteroids preying upon a suctorian (stalked sessile protozoan), which were often found in high densities on the blades of *Macrocystis*.

10. Fish predation on Lacuna vincta in the field

Field observations for the three years of this study suggested that predation pressure has the potential to exert a significant selective pressure upon *Lacuna vincta* in the subtidal area. Two embiotocids *Rhacochilus vacca* and

Embiotoca lateralis were common in Macrocystis and Nereocystis beds. These fishes, particularly R. vacca, were found to forage mainly on hard-shelled invertebrates. Stomach contents from five juvenile (8-9 cm) R. vacca caught in Macrocystis beds at Dixon Island on September 29, 1988, are listed in Table 2.3. Results show that R. vacca eats a vast array of shelled-preys, primarily gastropods (at least nine genera of snails) and bivalves (including clams, mussels, scallops), and one species of chiton. The small tube-building gastropod Petaloconchus montereyensis was the numerically dominant taxon eaten by the juvenile perch (Table 2.3). Lacuna spp. comprised between 1 and 25% of the total number of shelled prey items (mean: 6.9%). Shell fragments and opercula of Lacuna spp. were omnipresent in all five juvenile R. vacca sampled at Dixon Island Macrocystis bed, with 1-11 individual Lacuna spp. found per fish (Table 2.3). All prey items found in the gut were benthic undercanopy or low intertidal species, thus suggesting that R. vacca forages on benthos in Macrocystis beds.

11. Laboratory experiments on fish predation

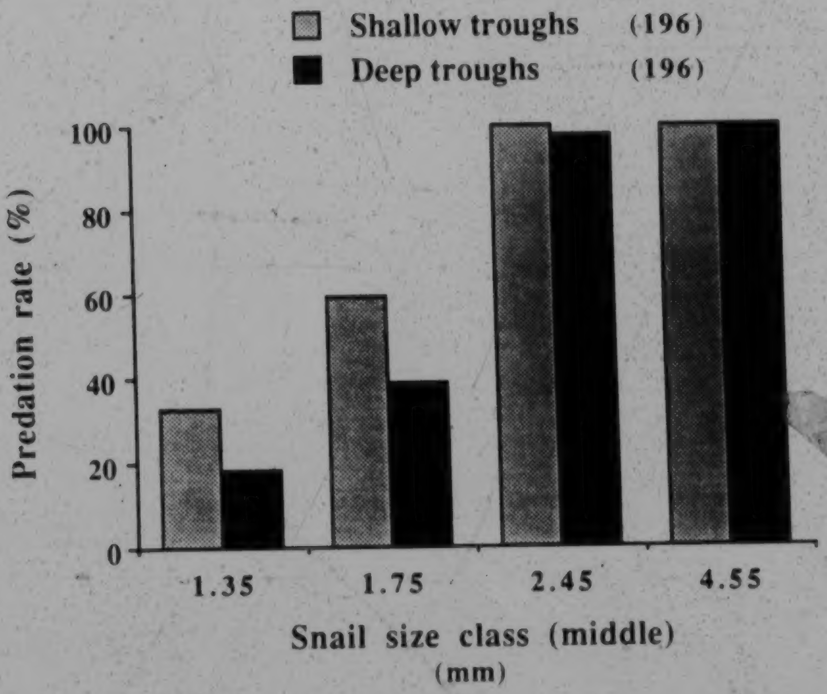
An increase in predation pressure by the embiotocid fishes with increasing snail size is shown in Figure 2.15. When fish were simultaneously offered four size classes of Lacuna vincta, larger individuals were avidly eaten whole by both R. vacca and E. lateralis and no shell fragments were expelled. Predation rates on large juvenile (2.0-2.9 mm) and

Table 2.3

Hard-shelled invertebrates found in the guts of five pile perch *Rhacochilus vacca* sampled by spear fishing using SCUBA. Site: *Macrocystis* bed at Dixon Island, on September 29, 1988. G = gastropods, B = bivalves.

		Fish #						
		1	2	3	4	5		
	Taxa	Number of invert.					N	%
G	Alvania spp.......	3	1	14	0	7	25	7.12
G	Crepidula spp.....	2	0	8	13	3	26	7.41
G	Gastropod spp.....	3	2	0	0	0	5	1.42
G	Lacuna spp........	4	5	3	1	11	24	6.84
G	Limpet spp........	4	0	7	1	5	17	4.84
G	Marguerites sp....	6	2	1	0	3	12	3.42
G	Petaloconchus.....	38	0	17	70	40	165	47.01
G	Tricolia pulloides	2	0	0	4	0	6	1.71
B	Clam spp..........	3	3	9	3	4	22	6.27
B	Hyatella spp......	0	0	0	2	3	5	1.42
B	Mytilus spp.......	0	9	0	3	4	16	4.56
B	Scallops spp......	0	0	5	3	16	24	6.84
	Chiton spp........	0	0	0	0	4	4	1.14
						Total =	351	

Figure 2.15. Relationship between shell length (mm) and *Macrocystis integrifolia* blade morphology on predation rates of *Rhacochilus vacca* and *Embiotoca lateralis* on *Lacuna vincta*. Histograms show percentages of snails eaten after 30 min. when placed into shallow (gray bars) or deep (black bars) troughs. Numbers in parenthesis indicate sample size (2 X 196; 49 individuals for each size class).


Shallow troughs (196)
Deep troughs (196)
Predation rate (%)
100
80
60
40
20
0
1.35
1.75
2.45
4.55
Snail size class (middle)
(mm)

adult *L. vincta* (4.0-5.1 mm) were nearly 100%. In contrast, smaller snails suffered significantly lower predation rates over the course of the experiments (30 minutes) (Kruskal Wallis ANOVA: $H = 83.62$, $p < 0.001$) (Fig. 2.15).

Predation rates were also affected by the type of *Macrocystis* blade on which juvenile *Lacuna vincta* were crawling (Fig. 2.15). During the experiments, significantly more juveniles were eaten by the two embiotocids when placed onto young blades with very shallow troughs than when placed onto mature blades with deep, well-formed troughs (Two-way ANOVA, $F = 4.656$, $p < 0.05$). This suggests that the use of troughs as shelter -- as observed in the field -- could help minimize predation on newly-metamorphosed juveniles.

D. DISCUSSION

1. Seasonality of oviposition

Lacuna vincta and *L. variegata* undergo a distinct seasonal spawning cycle, although egg masses can be observed year-round. Deposition of large numbers of egg masses on seaweeds, however, begins during late December-early January (Fig. 2.2). *L. vincta* found in the northeast Atlantic also begin spawning during January (Smith, 1973; Southgate, 1982; Grahame, 1986). Similar timing of spawning has been recorded in other *Lacuna* species (Rasmussen, 1973; Langan, 1984). Spawning possibly coincides with the shift in photoperiod. Pearse and Bosch (1987) demonstrated the crucial role of photoperiod in the regulation of gametogenesis in the antarctic asteroid _Odontaster validus_. In addition to gametogenesis, meso- and neogastropods have reproductive cycles that involve copulation, search for egg laying sites and oviposition (Martel _et al_., 1986 a, b). Yet, environmental factors associated with the timing of these events in _Lacuna_ spp. remain to be elucidated.

2. Abundance and growth of _Lacuna_ spp. larvae in the plankton

The abundance of _Lacuna_ spp. larvae (all sizes) in the plankton increases as they hatch from the egg masses during late winter (Fig. 2.2). At that time, there was a progressive increase in the number of _Lacuna_ spp. larvae in plankton samples taken at the offshore site (Edward King Island) (Fig. 2.3 A). At the time of settlement, however, overall densities of advanced veligers of _Lacuna_ spp. were similar at the offshore and the nearshore sites.

The study of size-frequency distributions of the _Lacuna_ spp. larvae during winter and spring have enabled us to estimate the duration of their planktonic period. From the peak of hatching during mid-February, to the time a distinct cohort of advanced, competent larvae is observed during late April, the veligers spend 7-9 weeks in the plankton. This estimation confirms that proposed by other authors in population studies on the same species: Smith (1973), 2-3 months; and Thomas and Page (1983), 2 months. Langan (1984) raised the larvae of _L_. _unifasciata_ and _L_. _marmorata_ in the laboratory and noted that metamorphosis occurs 38-55 days after hatching. Accurate estimates of the length of the planktonic period are difficult to obtain in nature, and for most marine benthic invertebrates these estimates come from studies conducted in the laboratory (gastropods: e.g. Perron, 1981; Chia and Koss, 1978, 1988; echinoderms: Strathmann, 1978; but see Barry, 1989). The study of larval cohorts in the plankton enabled an *in situ* determination of the duration of the planktonic period in *L. vincta*. In addition, this analysis has enabled a prediction of the timing and intensity of recruitment.

From the large numbers of *Lacuna* spp. larvae hatching during mid-winter and the length of time they spend in the plankton (7-9 weeks), one can speculate on the dispersal distance and the origin of competent larvae at the time of settlement. The Vancouver Island Coastal Current moves northward, nearshore, along the west coast of Vancouver Island (Thomson, 1981; Freeland *et al.*, 1984; Jamieson and Phillips, 1988). A current flowing in the same direction is also observed during the winter along the Oregon and Washington coasts (Davidson Current; Hickey, 1979). With these currents prevailing during the spawning period of *Lacuna* spp., it is possible that competent *Lacuna* spp. larvae in Barkley Sound during the spring originate from more southern localities. During a 2-month period, even assuming net average velocities as low as 5 cm / s, *Lacuna* spp. larvae transported by such currents have the potential to travel over 250 km. They could thus conceivably originate from the Washington coast or the Strait of Juan de Fuca/Georgia Strait area. No data are available, however, to support such speculation. Patterns and scale of dispersal of planktonic organisms depend on oceanographic conditions at the time the propagules are in the plankton, as well as on behaviour of the larvae in the water column (Strathmann, 1982; Legendre and Demers, 1984; Stancyk and Feller, 1986). Detailed studies on oceanographic conditions prevailing for differing spatial and temporal scales, coupled with data on in situ larval behavior, could answer these questions.

The observed size range at which Lacuna vincta larvae metamorphose (675-875 µm) differs from that reported for the same species in Europe. Fretter and Manly (1977) reported that the average smallest juvenile size class was 550 µm, although Southgate (1982) mentioned 450 µm for size at metamorphosis. Although it is possible that these geographically separate populations of L. vincta differ taxonomically, such differences in the size at metamorphosis could also be related to the variations in the amount of time the larvae spend in the plankton. Results from the present study suggest that a significant proportion of the larvae during the spring may have been delaying metamorphosis. In the sample of May 27, 1989, 23.9% of all the Lacuna spp. larvae collected were larger than 825 µm. Fretter and Shale (1973) have also reported that L. vincta larvae found in the region of Plymouth (England) can delay metamorphosis. In addition, Langan (1984) mentioned that L. unifasciata and L. marmorata larvae can delay metamorphosis for 18-26 days, during which time they continue to feed and grow. Delayed metamorphosis has also been reported for other gastropod species (Pechenik, 1984, 1985, 1986). Because Lacuna spp. larvae spend many weeks in the plankton, they may still be a great distance from the coast when they become competent. Therefore, it may be advantageous to be capable of delaying metamorphosis until coastal and tidal currents or internal waves (Shanks, 1983; Shanks and Wright, 1987) transport the larvae to coastal seaweed communities.

In addition to observations of recruitment in Macrocystis beds, data on temporal variations in the size-frequency distribution of Lacuna spp. veligers in the plankton during the spring of 1988 and 1989, suggest that the abnormally cold winter of 1989 may have significantly affected embryonic development, early larval growth and timing of peak recruitment. Unfortunately, recruitment rate was not quantified during 1989, and I am unable to make such comparisons. In a study on intertidal L. vincta, Smith (1973) observed that the lower winter seawater temperatures slowed intracapsular development. Even though spawning was spread over 4 months (winter-early spring), he observed that most hatching occurred over a 2-month period (May and June). Although seasonal and regional weather patterns likely influence rates of development of embryos and larvae, the effect of these factors on the timing and success of recruitment awaits further investigation.

3. Recruitment and abundance of advanced larvae

It is important to differentiate settlement from recruitment (Keough and Downes, 1982). In the cases of species where larvae settle and metamorphose at microscopic sizes, early post-settlement events may be overlooked until juveniles are large enough to be detected in the field by an observer. Keough and Downes (1982) showed that because of the mortality occurring between settlement and recruitment, the relationship between these two events can be weak. There are, however, studies reporting a closer relationship between recruitment and settlement (Yoshioka, 1982; Davis, 1987; Rumrill, 1987). Results from the present study show that Lacuna spp. larvae settle and metamorphose at large sizes on Macrocystis and Nereocystis blades, and can be immediately detected. Consequently, recruitment rate of L. vincta is proportional to the numbers of larvae that survive through settlement and metamorphosis -- the end of the larval life, or metamorphosis, in L. vincta is marked by the loss of the velum, which is ingested by the animal (Fretter, 1969, 1972).

Some studies on sessile organisms have emphasized the relationship between larval abundance and settlement rate (Grosberg, 1982; Yoshioka, 1982). Gaines et al., (1985) demonstrated that local concentrations of competent larvae of the barnacle Balanus glandula were reflected in the intensity of settlement. These results are consistent with my conclusions. Recruitment rates of Lacuna vincta in the Macrocystis bed canopy and abundance of advanced larvae in the plankton followed similar trends at two different sites (Figs. 2.5, 2.6) (although not as clear during the summer of 1988). The settlement of L. vincta in the Nereocystis canopy also followed a pattern similar to that observed in Macrocystis, although it occurred at a much lower rate (Fig. 2.6). These results emphasize the importance of assessing the abundance of competent larvae arriving in the habitat as a determinant factor controlling recruitment rates.

4. Migration of juveniles towards the benthos

Two plausible explanations arise for the observed decrease in density of juvenile Lacuna vincta occurring soon after the peak of recruitment, as well as for the year-round persistence of small juveniles and their apparent absence of growth in the canopy. These are: (1) that juveniles are subject to heavy mortality soon after metamorphosis, or (2) that juveniles migrate away from the canopy after a brief period of growth. Early juvenile mortality has the potential to influence strongly patterns of recruitment in benthic marine invertebrates (Cameron and Schroeter, 1980; Keough and Downes, 1982; Luckenbach, 1984; Young and Chia, 1984; Connell 1985; Jensen and Jensen, 1985; Rowley, 1989). Results presented in this study suggest, however, that mortality is not responsible for the decline in density following recruitment, nor does it explain the unique size distribution observed in the kelp canopy.

I hypothesize that newly-metamorphosed *Lacuna vincta* migrate toward the benthos after 1-3 weeks of growth in the *Macrocystis* canopy. Several lines of evidence support this hypothesis: (1) SCUBA observations of juveniles drifting in the water column, (2) high numbers of juveniles trapped in off-bottom kelp collectors, (3) similarity between the size distribution of drifting juveniles and those found in the canopy, (4) the differential vertical size distribution of juveniles along the fronds of *Macrocystis* and (5) the comparison between the size-frequency distributions of juveniles found in the canopy versus the undercanopy during recruitment periods.

A depth-related difference in size distribution, like that observed at the protected bed at Diana Island during 1988 and 1989, is consistent with the hypothesis of a downward migration which would occur when juveniles leave their original habitat (canopy) shortly after larval settlement and metamorphosis (2-3 weeks). Observations suggest that newly-metamorphosed *Lacuna* spp. do not crawl onto the stipe of *Macrocystis* fronds. Thus, it is possible that juveniles move downward from blade to blade, particularly at low tide when blades are more often in close contact. As suggested by the large number of juvenile *L. vincta* in collectors, however, such migration or displacement could also be accomplished by drifting (see Table 2.2, Fig. 2.11). The high dispersal capability of post-metamorphic stages of Lacuna spp. has recently been demonstrated (Johnson and Mann, 1986; Martel, 1987, 1988; present study, see Chapter III and IV). Rapid growth rates, with juveniles attaining 1 mm about 1 week after metamorphosis, (see Chapter IV) could mean that if juveniles reach the undercanopy seaweeds through consecutive drop offs and landings on the lower level blades, over a period of several days, many of them can grow to larger sizes by the time they reach the benthos (Figs. 2.10, 2.12).

It is noteworthy to mention that the depth-related difference in size distribution of juvenile Lacuna vincta was more pronounced at the protected Macrocystis bed at Diana Island than at Dixon Island. In addition, for both sites, this pattern was also more clearly elucidated during the fall than during the spring (Figs. 2.12, 2.13). The fully grown plants present during the fall, which are taller and have many more rows of blades than plants growing during the spring (Figs. 2.12, 2.13) potentially constitute a more favorable environment for the establishment of a vertically-related size-distribution pattern. Both hydrodynamics and frond shape may influence the vertical distribution of juvenile Lacuna spp. on Macrocystis.

Alternatively, it could be hypothesized that Macrocystis fronds grow quickly enough that new blades could have been exposed to larval settlement for a much shorter period of time than mature blades. However, the 2 to 3 weeks necessary for juveniles to grow from about 0.85 to 1.3 mm (size range observed in the canopy) (see data on growth rates of juvenile Lacuna vincta, Chapter IV) is less than the time required for a frond to grow 3 to 4 meters in length (6 to 8 weeks during spring, Lobban, 1978). Thus frond growth may be too slow to explain such a vertical pattern of size distribution.

One could also propose that growth rates of juvenile Lacuna vincta differ depending on the region of the frond (blade age or position) on which it is feeding. Yet, no indication of such differential growth has been observed in laboratory experiments when juveniles were fed mature blades from different frond sections. Moreover, such patterns of size distribution did not occur along cultivated Macrocystis fronds growing horizontally at the kelp farm (Martel, unpublished). These observations, coupled with results on drifting, support the hypothesis that the vertical size-distribution pattern is the result of a migration of juveniles from the canopy to the bottom. Although findings seem to support the migration theory, further experiments involving marking and release/recapture techniques are needed before an unequivocal explanation for this pattern can be identified. Such an investigation should also include the study of patterns of abundance of competent larvae along a vertical gradient when L. vincta veligers settle in the canopy.

The abundance of substrate patches devoid of seaweeds in the undercanopy implies that high numbers of drifting Lacuna vincta may not reach suitable substrata (algae) upon arrival on the bottom. Although the snails are capable of crawling on various substrata, a distance of only a few meters devoid of seaweeds (sand, cobbles, gravel) could represent a considerable barrier preventing the tiny juveniles from reaching a suitable habitat. In this way, drifting may result in high juvenile mortality. The discovery of numerous intact dead juveniles (shells) of 1.5-1.75 mm shell length in air-lift samples taken from patches devoid of seaweeds supports this hypothesis (Martel, unpublished). Quantitative assessments of mortality associated with drifting in *Lacuna* spp. are unavailable and warrant further investigation.

5. Predation: a potential selective pressure

The vulnerability of intertidal and shallow subtidal gastropods to predation by certain fish species has been well documented (Vermeij, 1978; Reimchen, 1979; Palmer, 1979; Ortega, 1986; Johnson and Mann, 1986; Shepherd and Turner, 1985; Norton, 1988). Additional studies have confirmed the role of fish predation in subtidal benthic invertebrate communities of *Macrocystis pyrifera* beds in California (Bernstein and Jung, 1979; Tegner and Dayton, 1981; Keough and Downes, 1982). The perch *Rhacochilus vacca* and *Embiotoca lateralis* are two of the most common inshore fishes along the Pacific Coast of North America (Haldorson and Moser, 1979). They have been reported to prey upon a wide variety of shelled invertebrates (Haldorson and Moser, 1979; Ellison *et al*., 1979). Brett (1978) demonstrated how *R. vacca* is superbly adapted to feeding on hard-shelled prey, such as mussels, which are ingested whole and then crushed by powerful pharyngeal teeth. I have observed these fishes during most dives in Nereocystis and Macrocystis beds between April and December. In the present study, results show that gastropods represent an important component of the diet of R. vacca (Table 2.3). The presence of nine gastropod genera, in addition to many bivalves species, in the stomach contents of R. vacca indicates that this fish is a non-selective predator feeding on a large number of small molluscs, including Lacuna vincta. Haldorson and Moser (1979) reported similar findings and also mentioned that many of the prey of R. vacca and E. lateralis are associated with algae. Opercula and shell fragments of large juvenile and adult L. vincta are commonly found in fecal pellets of R. vacca (present study; Martel, unpublished). Thus, data from stomach and fecal pellet contents suggest that fish could exert a selective pressure upon many gastropods, including L. vincta.

It may well be that leaving the canopy habitat is an adaptive response of juveniles to their increasing vulnerability to visual predators. Although fish predation on Lacuna spp. is likely important in the subtidal undercanopy (see Table 2.3), it is possible that predation rates on individuals that would grow and remain in the Macrocystis canopy would be higher. As newly-metamorphosed juveniles reach sizes > 1 mm they may not be able to find suitable shelters inside the shallow (0.5-1.5 mm) troughs of

Macrocystis blades. Laboratory experiments indicate that Rhacochilus vacca and Embiotoca lateralis did not eat, and may have overlooked juvenile Lacuna vincta < 1 mm shell length, even after 24 hours (Martel, unpublished). However, predation rates increased rapidly as juvenile size increased (18-33% for juveniles of 1.2-1.5 mm shell length and 98-100% for individuals > 2 mm) (Fig. 2.15). Shepherd and Turner (1985) reported an increased vulnerability to fish predation by wrasses as juvenile Haliotis spp. reached sizes ≥ 5 mm. In a study on Littorina sitkana conducted in Barkley Sound McCormack (1982) mentioned that the perch R. vacca preferred large juveniles and adults.

Further experiments indicated that while newly-metamorphosed juvenile Lacuna vincta appear unaffected by blade movement, large juveniles and adults tend to drop more easily off blades subject to continuous motion (Martel, unpublished). Motion of kelp blades (via tidal currents, waves or surge) may prevent large L. vincta from finding shelter and remaining cryptic between blades, rendering them vulnerable to predation (Reimchen, 1979; Mercurio et al., 1985). Such shelter is likely available among the seaweeds of the undercanopy where large juvenile and adult L. vincta are found.

The real impact of fish predation on populations of juvenile Lacuna vincta found in the Macrocystis canopy is unknown and, although the information reported here confirms juvenile drifting as a means of dispersing away from the canopy, one cannot completely exclude the possibility that predation is responsible for the disappearance of juveniles from the kelp bed canopy following spring recruitment. Although no fish were observed preying upon newly-metamorphosed juveniles, it is possible that because SCUBA observations were made during the day, nocturnal predatory fish went undetected. In the present study, newly-metamorphosed juvenile *L. vincta* were found in the guts of two out of five penpoint gunnel, *Apodichthys flavidus*, caught among the undercanopy seaweeds in a *Macrocystis* bed. Thus, *Lacuna* spp. could be part of the diet of a variety of fish species (see Norton [1988] on the presence of *Lacuna* spp. in stomach contents of sculpins). More studies will be needed to address the question of juvenile mortality associated with predation in kelp beds.

It is appropriate to mention the pattern of habitat-use by the trochid *Tegula pulligo*, another gastropod in *Macrocystis* beds. This large, thick-shelled species utilizes *Macrocystis* beds in a way opposite to that of *Lacuna vincta*. While small juvenile *T. pulligo* are primarily found in the undercanopy, only large individuals and adults move up onto the stipes and blades of *Macrocystis* (Sharp, 1974; Watanabe, 1984; Martel, pers. obs.). Large juvenile and adult *T. pulligo* graze in the canopy of *Macrocystis* (Sharp, 1974; Watanabe, 1984), where they often cause significant damage (Sharp, 1974). Adult *T. pulligo* have a larger, strong conical shell. Laboratory and field observations suggest that the thickness, shape and particulary the size of T. pulligo's shell effectively deter predation by embiotocids (Martel, unpublished). Such drastic differences in adult shell size and thickness between the two snails (20-30 mm compared with 4-8 mm for L. vincta) suggest differences in vulnerability to fish predation and may explain the opposite patterns of habitat use between these two gastropods.

6. Macrocystis bed canopy: a nursery habitat

The use of nursery grounds by early life stages has been demonstrated in many aquatic organisms, including marine benthic invertebrates (Kneib, 1987 a, b) and fish (Kneib, 1987 a; Mittelbach, 1981; Werner *et al*., 1983). Seaweeds have been shown to constitute an important habitat used by many benthic marine invertebrate larvae at settlement (e.g. crustaceans: Marx and Herrnkind, 1985; Herrnkind and Butler, 1986; gastropods: Sarver, 1979; asteroids: Barker, 1979). After a variable period of growth, the juveniles then migrate to the adult habitat.

Macrocystis beds cover vast areas along the outer coast of British Columbia including Barkley Sound (Wheeler and Druehl, 1986). They create a transition between the open water and the benthic shallow subtidal and intertidal zones, forming dense habitats with an important exposed surface area for larval settlement. The abundance and density of Macrocystis blades could make the canopy habitat a larval collector or filter (Bernstein and Jung, 1979) for many species, the larvae of which do not have specific substratum requirements.

Larvae and newly-metamorphosed juveniles of invertebrates other than *Lacuna vincta* also utilize the canopy of *Macrocystis* beds. For example, newly-metamorphosed juveniles of the neogastropod *Alia* (=*Mitrella*) sp. and of one, possibly two, unidentified asteroids have been found in the canopy. Following metamorphosis and a short period of growth, juveniles may be able to crawl down or drop off from the canopy to recruit in the undercanopy. Moreover, since the blades of *Macrocystis* are short-lived, the degradation and death of the plant tissues could also result in these invertebrates falling and recruiting to the benthos. Such a pattern of habitat use has been reported by Herrlinger *et al.* (1987), who observed high numbers of juveniles of the asteroid *Pisaster giganteus* in the canopy of *Macrocystis pyrifera* beds in California. They reported higher densities of juvenile asteroids per m^2 of canopy (water column) than per m^2 of sea bottom, and suggested that settlement likely occurred on the blades. They hypothesized that juvenile *P. giganteus* subsequently fall off or crawl down to the kelp forest floor where large juveniles and adults are found.

Detritus and epiphytic microorganisms, such as bacteria, diatoms and protozoans, are particularly abundant on mature and senescing kelp blades (Laylock, 1974; Albright *et al.*, 1980) and may represent an excellent food source for post-larvae and newly-metamorphosed juveniles of a variety of marine invertebrate species. High densities of suctorian protozoans often occur on the blades of Macrocystis (Martel, unpublished) and my observations suggest that these organisms could represent part of the diet of juvenile asteroids in the canopy. Also, compared with the undercanopy or benthic environment, the canopy habitat may allow for higher growth and/or lower mortality rates of early life stages, thus making this habitat an effective nursery ground. We must exercise caution, however, when studying benthic invertebrates utilizing kelp bed canopies because post-larvae and newly-metamorphosed juveniles may use this habitat for a very short period of time (hours, days or weeks). Too small to be seen with the naked eye, the larvae may settle, metamorphose in the canopy and disappear long before an observer can count them. Thus, the short-term use of kelp canopies, followed by post-metamorphic movements may be parts of the life history of many non- sessile benthic invertebrates. Clearly, such factors are capable of affecting spatial and temporal patterns of distribution and abundance. Their effects on recruitment warrant further detailed investigations.

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CHAPTER III.

MUCOUS DRIFTING AS A DISPERSAL MECHANISM IN BENTHIC MARINE INVERTEBRATES

A. INTRODUCTION

A ubiquitous component of the life history of organisms is their ability to disperse (Hamilton and May, 1977). For many benthic marine invertebrates, the planktonic larval stage is the primary agent of dispersal (Strathmann, 1974; Jablonski and Lutz, 1983). In general, species lacking a planktonic larval stage have limited dispersal (Mileikovsky, 1971; Jablonski, 1986; Scheltema, 1986). Thus, benthic marine invertebrates with direct development (those which brood or produce benthic egg capsules with crawl-away juveniles) should have a reduced dispersal potential, and a restricted geographical distribution (Jablonski, 1986; Scheltema, 1986; Jablonski, 1987; Scheltema, 1989). Yet, many species with direct development are widely-distributed (Ponder, 1971; Simpson, 1977; Pearse, 1979; Morris _et_ _al_., 1980; Kozloff, 1983; Johannesson, 1988; O'Foighil, 1989). Some even have a wider geographic distribution than those species in the same genus with a planktonic larval stage (Johannesson, 1988; O'Foighil, 1989), suggesting that alternative and effective methods of dispersal exist.

One such method is floating or rafting (Dell, 1972; Arnauld _et_ _al_., 1976; Highsmith, 1985) accomplished by juveniles, or, in the case of small-sized organisms, adults

(Strathmann and Strathmann, 1982). In the small gastropods of the genus Hydrobia, floating using surface tension allows local dispersal (Anderson, 1971; Little and Nix, 1976; Levinton, 1979). Other gastropods such as the pelagic Janthina spp. live, feed and disperse at the water surface by producing a mucous raft containing air bubbles (Morton, 1979). The method of dispersal in many widely-distributed marine benthic invertebrates with direct development, however, is unascertained and remains speculative.

Here, I present quantitative evidence that several widely-distributed marine benthic invertebrate species lacking a planktonic larval stage invoke an effective alternative method of dispersal. This dispersal is achieved by juveniles and small adults drifting in the water column.

Post-larval and juvenile drifting using byssal and mucous threads has been demonstrated in many bivalves, including mussels (Sigurdsson et al., 1976; de Block and Tan-Maas, 1977; Lane et al., 1982, 1985) as well as marine and freshwater clams (Sigurdsson et al., 1976; Sigurdsson, 1980; Beukema and de Vlas, 1989; Prezant and Chalermwat, 1984). According to Sigurdsson et al. (1976), this behaviour is analogous to the gossamer flight of young spiders. In the marine invertebrates mentioned above, microscopically thin mucous threads many times the length of the animal increase hydrodynamic drag on the juveniles and enable them to be lifted and transported in the water column by currents (Sigurdsson et al., 1976; Lane et al., 1985). The work presented here specifically examines the role of mucous threads in the dispersal of post-metamorphic gastropods and bivalves.

The significance of juvenile drifting as a mechanism for dispersal and recruitment by marine molluscs is poorly understood. Bayne's (1964) study originally demonstrated how juvenile Mytilus edulis can disperse and colonize habitats where larval settlement had been low or absent. More recently, Beukema and de Vlas (1989) reported that post-metamorphic drifting is an important recruitment mechanism in the clam Macoma balthica and they mentioned the transport, by currents, of juveniles using byssal threads.

Post-metamorphic drifting has also been reported for gastropod species (Sigurdsson, 1980). Vahl (1983) noted that the limpet Helcion pellucidus found on the kelp Laminaria hyperborea, when dislodged by waves, may produce mucus in copious amounts which acts as a "sticky sail giving the limpet a nearly neutral buoyancy and enables the snail to rapidly recolonize its habitat" (Vahl, 1983). In a study on the ecology of subtidal Laminaria longicruris beds in Nova Scotia, Johnson and Mann (1986) described how the gastropod Lacuna vincta can disperse between blades. Also, I have observed L. vincta drifting and have tested its significance in the recruitment of the snail in Macrocystis beds and subtidal undercanopy habitats on the west coast of Vancouver Island (Martel, 1987; see Chapter II).

The present study has three specific objectives. The first is to demonstrate that several marine benthic invertebrates lacking a planktonic larval stage can disperse by drifting. I report here, for the first time, quantitative evidence of frequent water-column drifting in several common brooding invertebrates (mostly molluscs) of the eastern Pacific Ocean. These include the intertidal brooding bivalves *Musculus* sp., *Lasaea* sp. and *Transennella tantilla*, as well as the small gastropod *Barleeia* spp., which produces benthic egg capsules and crawl-away juveniles. Other taxa, including species with a planktonic larval stage, have also been found drifting in large numbers as juveniles. This is shown by using off-bottom collectors placed in semi-exposed rocky intertidal and nearshore areas. One of the main factors that contributed to the success obtained in collecting high numbers of these drifting benthic invertebrates is that collectors were made of a substratum that mimics one of their natural habitats: the red algal turf.

The second objective of this study is to demonstrate that drifting can be initiated voluntarily by snails and is not just a consequence of accidental dislodgement. This is shown for *Lacuna* spp. by recording the unique foot-raising behaviour and the release of a mucous thread just before the animals leave the substratum.

Finally, I investigate several properties of mucous threads produced by drifting *Lacuna*. The length of the drifting thread, its effect on sinking rates of snails, and its property for enhancing the animal's ability to attach to nearby substrata while drifting, are reported. The structure of the drifting mucous threads of Lacuna spp., as well as of those of Barleeia spp., were examined under phase-contrast and scanning electron microscopy, and compared to the mucous thread of a non-drifter, the gastropod Alia (=Mitrella) gouldi. The function and structure of these two different types of mucous threads are discussed in light of the life-history of these gastropods.

B. MATERIALS AND METHODS

1. Study area

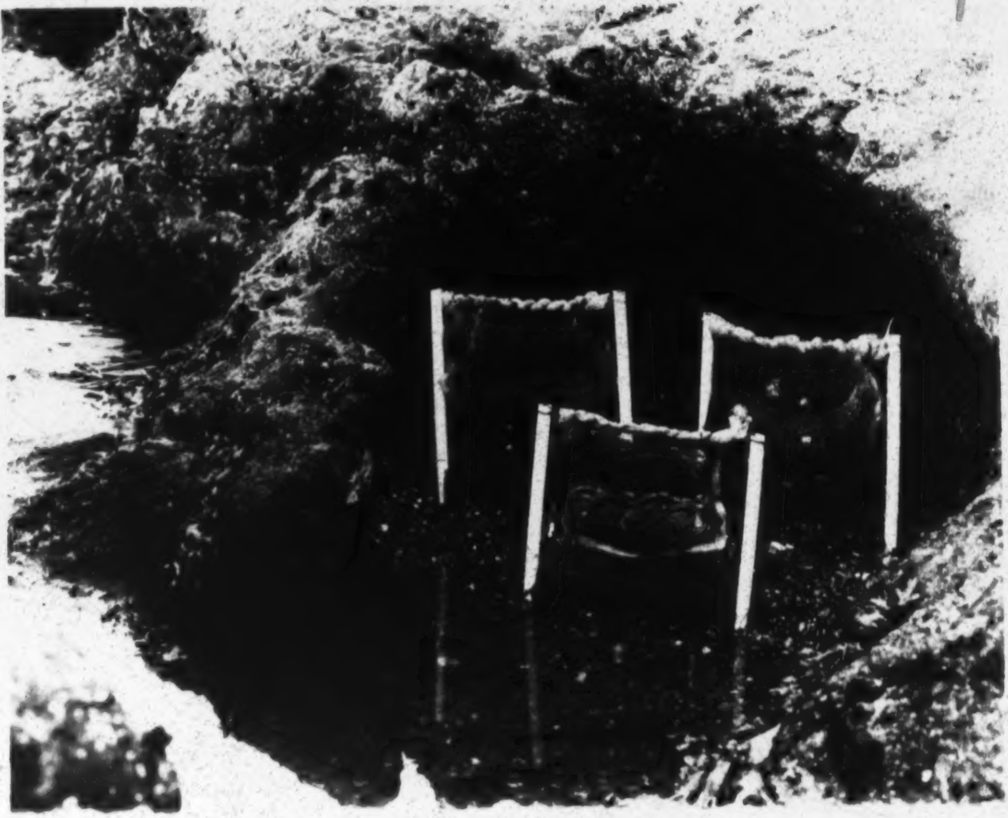
The study was carried out at Prasiola Point, in Trevor Channel (Fig. 2.1, see Chapter II). This semi-exposed rocky shore is subject to year-round moderate to strong wave action and to westerly and northwesterly winds. Offshore winds and swell make sampling in the low intertidal zone difficult and sometimes impossible. The rocky intertidal zone is characterized by diverse rocky intertidal seaweed communities that harbour many species of non-sessile invertebrates, including small bivalves and gastropods.

2. Intertidal off-bottom collectors

Collectors were designed to mimic a habitat used by many molluscs common to the rocky intertidal zone. Gracilaria pacifica was placed in nylon bags suspended in the intertidal zone to create a natural and complex substratum physically similar to the dominant red algal turf community. Approximately 200 g (wet weight) of G. pacifica was placed in large-mesh (9 mm) nylon bags (40 X 25cm) and then suspended from PVC pipes (height = 45 cm) via a thin wire. The pipes were either bolted to large bricks buried among the boulders of the intertidal zone (Type I) (Fig. 3.1) or cemented directly to the bedrock with splash-zone epoxy (Z-Spar, type II). Gracilaria pacifica rather than red turf algae was used because it is morphologically more robust, yet still creates a natural and similar complex substratum. It was collected at low tide in Grappler Inlet (Fig. 2.1, see Chapter II). Before being placed in the collector, it was washed four times in warm (30-40° C) freshwater to remove all gastropods, bivalves and other invertebrates.

Between four and six collectors were installed in surge channels (2-3 collectors per channel) where seaweeds were particularly abundant in the summer. All seaweeds were removed within a radius of 40-100 cm from the collectors, thus ensuring that animals could not crawl in from surrounding plants. Regular inspection of the collectors confirmed that no invertebrates were found crawling on the PVC pipes or on the attachment wire. After 24 hours the bags were removed from the pipes, washed three times in freshwater, and returned. Invertebrates removed by this freshwater treatment were recovered by filtration and taken to the laboratory for analysis.

Figure 3.1. Off-bottom collectors (type I) installed in a semi-exposed low intertidal area at Prasiola Point during the summer of 1989. Note the surge channel and abundance of seaweeds to the left.



Collectors were set up during three consecutive seasons: spring (May), summer (August) and late fall (November) of 1988. For each season, they were installed for up to 10 days (tides and sea conditions permitting).

Confirmation of direct development in small brooding bivalves caught in collectors was verified under a dissecting microscope by characterizing the type of prodissoconch structures (see Ockelmann, 1965; O'Foighil, 1989). Amphipods and isopods trapped by collectors were not censused in this study. The taxonomy used to identify invertebrates caught in off-bottom collectors followed that of Kozloff (1987).

3. Effects of hydrodynamic conditions and type of substratum on abundance of drifters in collectors.

Water flow between the two intertidal collection sites was determined in situ by measuring dissolution rate of sugar candies (Life-Savers) (see Koehl and Alberte, 1988). Water flow was determined by fastening pre-weighed ($\pm$ 0.0001 g) Life-Savers (peppermint) to the end of a 3 m stick placed beside the collectors 1-2 h before high tide. Life-Savers were left for five minutes, after which time they were removed and individually placed in separate vials. Between eight and eleven replicate Life-Savers were immersed for each site. This experiment was conducted during relatively calm sea conditions (swell < 1 m) on July 04, 1989. In the laboratory, individual Life-Savers were blotted and re-weighed and the weight loss was calculated. A standard curve relating weight loss of Life-Saver with water flow was determined by using a flow tank filled with running seawater of identical temperature to that measured in the field.

To assess the ability of collectors made with the red alga Gracilaria pacifica to capture and retain certain marine invertebrates, control collectors were installed. They were made with Kinran, a commercially-available material made of numerous monofilament threads (10-12 cm long) projecting omnidirectionally from a core rope. This type of substratum is used by the Japanese for settlement of bivalve larvae, notably scallops. Each control collector contained 70 cm of Kinran rope, and represented approximately 11,000 cm^2 of surface area for settlement. This represented about 3 times more surface area than the Gracilaria collectors (3200-4000 cm^2; estimated from the relationship between wet weight and surface area of the plant).

4. Offshore collectors

To determine whether small molluscs, particularly brooders, can be found drifting offshore, collector bags identical to those used in the intertidal zone were immersed 1-3 m below the surface in the bay, off Prasiola Point (Fig. 2.1, see Chapter II). A total of seven collectors were attached to four separate anchor lines (1-2 bags per anchor) placed parallel to the shore. Anchor lines on which the collectors had been tied were 20-30 m from the shoreline and 10-20 m apart. The depth at the site was 8-11 m, above a sandy substratum. Collectors were left for a period of five days and the experiment was repeated three times between June 14 and July 01, 1989. The procedures for extraction of invertebrates from the collectors were identical to those described earlier.

5. Production of mucous threads

a. Behaviour of Lacuna spp. and initiation of drifting

The behaviour of Lacuna vincta and L. variegata initiating drifting and producing mucous threads was studied in a low-velocity surge tank (90 cm long X 90 cm wide X 35 cm deep). The oscillating flow was adjusted to 9-11 s / cycle, with corresponding peak velocities of 15-25 cm / s. An individual Lacuna (1.5-3 mm shell length) was placed on a 2 cm long piece of the eelgrass Zostera marina, which was glued in a horizontal position on top of a Plexiglas TM podium. The podium with the snail on top was placed in the middle of the water column of the flow chamber. An RCA-BW video camera equipped with a 55 mm macro Nikkor lens (35 mm format) was set up against the plexiglass window of the tank in order to have a full frame view of the eelgrass and snail. Three incandescent 100 watt lamps were distributed both beside and behind the tank to help illuminate the mucus by refraction of the light beams.

b. Length of mucous threads in Lacuna vincta

To estimate the length of the mucous thread of drifting Lacuna vincta, snails were placed on a small piece of turf algae (Gracilaria pacifica), which was then immersed and attached in the flow tank. With the water flow adjusted at 2-2.5 cm / s , the snail was gently dislodged from the alga with a pair of forceps. The snail remained linked to the alga by its mucous thread, preventing it from being transported by the water current. The snail, with its stretching thread, was left in this position until the mucous thread ruptured, and the snail was transported by the water current. The distance between the snail and the alga just before the mucous thread broke was used as the maximum length at which the mucous thread was capable of holding the snail in the water flow. L. vincta of shell length ranging from 1.3 to 5.6 mm were used to test for possible effects of size on the length of mucous thread produced.

6. Importance of mucous thread on sinking rates

The effect of mucus on snail sinking rates was studied using a transparent Plexiglas TM cylinder (height: 120 cm, diam.: 10 cm) to which was attached a 1 m ruler. The cylinder was filled with seawater ($T = 10^{o}$ C). Adult and juvenile Lacuna variegata were placed individually in a finger bowl and gently spun for a few seconds. This method was found to induce the formation of the mucous thread effectively. The snail was then dropped in the middle of the cylinder with a minimal amount of water disturbance. The time required by the sinking snail to cross the bottom 50-80 cm of the cylinder was recorded. This allowed enough time for the dropped snail to reach its terminal velocity (usually within the first few cm of the water column).

To compare sinking rates of individual Lacuna variegata without mucous threads, snails were blotted with a paper towel, held by the sides of the shell with forceps and dropped directly in the middle of the cylinder. Although the snail would rapidly extend its foot and antennae during the first few cm of the descent, in most cases no mucous thread was produced. Serving as controls, sinking rates of snails withdrawn into their shells were studied by using individuals that had been placed in a dilute formalin-seawater solution for several minutes, thus forcing the snails to remain withdrawn into their shell during the course of the experiment.

Because simulated water currents were not effective in inducing the formation of mucous threads in the gastropods Littorina sitkana and Nucella emarginata, I used a different procedure. Snails were placed on a glass slide and allowed to hold on and crawl for a few seconds. The glass was then immersed in the top few cm of the filled cylinder and the snail gently dislodged with a pair of forceps. In most cases this method induced the stretching of mucus already present under the foot and the formation of a thread. The procedure used for control (withdrawn) snails is the same as that used for Lacuna variegata.

7. Mucous threads and attachment to substratum while drifting

The ability of Lacuna vincta to attach to the substratum while drifting was tested by placing a plastic screen (9 X 15 cm; thickness: 1 mm) with square holes of 9 mm and placed vertically across the flow chamber of a flow tank (velocity adjusted to 15 cm / s). Snails between 2.5 and 6 mm shell length were put individually into a finger bowl filled with seawater and gently spun with a pair of forceps for a few seconds. The snail was then poured out of the bowl into the flow tank (15-20 cm ahead of the plastic screen) and allowed to drift with its mucous thread. As the snail passed through the screen the thread was usually caught. The ability of the thread to retain the snail once caught in the screen was recorded. A negative result occurred when the drifting snail carried by the current passed directly through the screen without becoming attached. In a second treatment, snails were dropped into the tank by holding the sides of the shell with forceps without allowing the foot to contact anything. With this technique, most snails could not rapidly produce a mucous thread but were usually capable of protruding their foot while being carried by the currents. The ability of these snails to become attached to the screen with their extended foot was determined. Finally, withdrawn snails that had been out of the water for a 10-15 minutes were used as controls.

8. Structure of mucous threads

a. Mucous threads used by drifters: Lacuna spp. and Barleeia spp.

To study the structure of the mucous thread of drifting snails, Lacuna vincta and Barleeia sp. were put in a finger bowl and stimulated to produce mucous threads. They were then poured into a tank and allowed to drift. A microscope slide was then used to raise the snail by its thread. Lifting the snail out of the water usually ruptured the thread at both edges of the slide. The retained piece of thread was air dried for 10-15 minutes, then rinsed with distilled water, air dried again and then observed under a Leitz phase contrast microscope.

b. Mucous threads used by a non-drifter: Alia gouldi

The thread of the non-drifter Alia gouldi was studied by allowing snails to crawl on a microscope slide immersed in a finger bowl. Pieces of mucous thread from A. gouldi hanging from Zostera blades in holding tanks were also sampled using the same technique as for Lacuna vincta and Barleeia sp..

C. RESULTS

1. Invertebrates found drifting in intertidal collectors

All but one of the 18 taxa found drifting in the water column at high tide are molluscs (Table 3.1). Most striking in this list is the presence of at least eight species (four gastropods, three bivalves and one asteroid) that lack a planktonic larval stage (Table 3.1, Fig. 3.2). The

Table 3.1

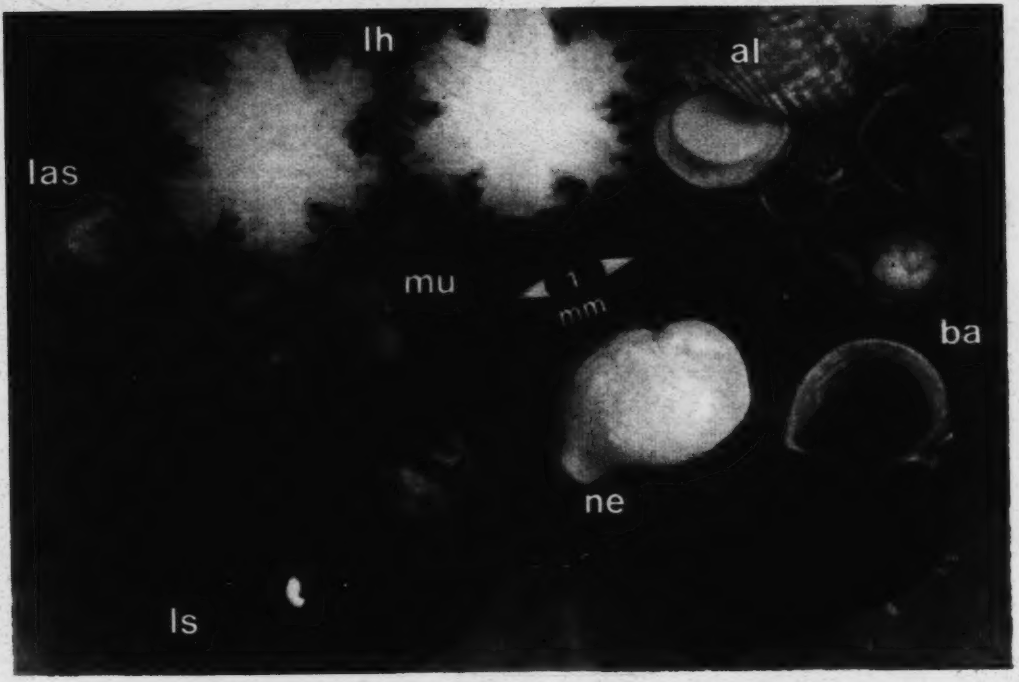
Post-metamorphic benthic invertebrates trapped in off-bottom intertidal collectors at Prasiola Point in 1988. List includes 18 taxa (17 molluscs and one echinoderm).

Type	Repro. mode	Taxa found in Collectors	Avg/coll/day			Tot. (n)	Avg. Size (mm)
			Spr	Sum	Fall		
Ga	L	Lacuna spp...........	30.20	6.00	12.50	781	1.48
Bi	L	Mytilus spp..........	1.05	12.00	14.33	311	1.58
Ga	DE	Barleeia spp.........	2.60	2.24	2.00	102	1.32
Bi	DB	Musculus sp..........	0.40	3.24	0.33	65	0.80
1 Ga	?	Tricolia pulloides...	0.15	1.41	0.50	30	1.05
Ga	L	Littorina scutulata..	0.75	0.29	0.33	22	3.05
Ga	L	Limpet spp...........	0.20	0.82	0.50	21	1.44
Bi	DB	Lasaea sp............	0.10	0.82	0.33	18	0.79
Bi	DB	Transennella tantilla	0.20	0.00	0.83	9	2.64
Bi	L	Hiatella arctica.....	0.00	0.47	0.00	8	1.20
Bi	L	Clam spp.............	0.20	0.12	0.00	6	0.54
2 Ga	?	Alvania spp..........	0.10	0.06	0.17	4	0.60
As	DB	Leptasterias hexactis	0.15	0.00	0.00	3	0.69
2 Ga	?	Margarites sp........	0.00	0.18	0.00	3	3.05
Ga	DE	Onchidella borealis..	0.00	0.12	0.17	3	4.22
Ga	DE	Nucella emarginata...	0.00	0.12	0.00	2	1.28
Ga	DE	Littorina sitkana....	0.05	0.00	0.17	2	2.73
Ga	L	Alia gouldi..........	0.05	0.00	0.00	1	7.92
		Collector days (n)	20	17	6		
		Average wave height (m)	0.3	0.4	2.0		
		Average swell (rank)	1.2	1.0	2.8		

Type: Ga = gastropod, Bi = bivalve, As = asteroid

Reproductive mode:
L = With planktonic larval stage
DE = Direct development: egg capsules and crawl-away juv.
DB = Direct development: brooding
1 = Mooers (1981) reported direct development in *Tricolia pulloides* in Pacific Grove, California.
2 = Reproductive mode unknown

Figure 3.2. Several of the post-metamorphic invertebrates caught in off-bottom intertidal collectors at Prasiola Point. Top: some of the species with direct development (lacking a planktonic larval stage). Bottom: five of the most common species caught in off-bottom intertidal collectors (include species with and without a planktonic larval stage; see Table 3.1).
al = *Alvania* sp.; ba = *Barleeia* spp.; lac = *Lacuna* spp.;
las = *Lasaea* sp.; lh = *Leptasterias hexactis*;
ls = *Littorina sitkana*; mu = *Musculus* sp.;
my = *Mytilus* spp.; ne = *Nucella emarginata*;
tp = *Tricolia pulloides*.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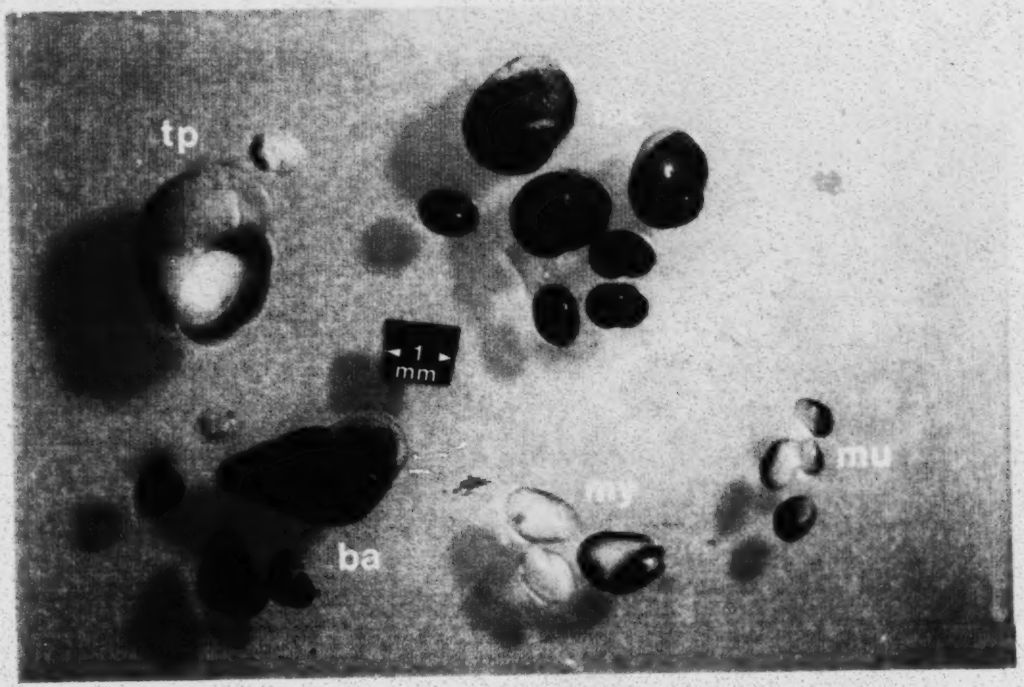
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prosobranch gastropod Barleeia spp., which produces benthic egg capsules with crawl-away juveniles (confirmed in the laboratory) and the brooding bivalve Musculus sp. were among the most abundant drifting species found in the collectors (Tables 3.1, 3.2, Fig. 3.2). During the summer, at site A, a daily average of 3.5 Barleeia spp. (highest = 8) and 5.3 Musculus sp. (highest = 10) were found per collector (Fig. 3.3). Two other brooding bivalves, Lasaea sp. and Transennella tantilla, have also been found drifting, with averages up to 1.2 (highest = 6) and 1.7 (highest = 4) individuals / collector / day, respectively (Tables 3.1, 3.2; Fig. 3.2).

Ranking 5th in order of abundance, a total of 30 Tricolia pulloides (Carpenter, 1865) (mostly juveniles; see Tables 3.1, 3.2, Fig. 3.2) were trapped in off-bottom intertidal collectors. I did not confirm the mode of development of this species but Mooers (1981) mentioned direct development in T. pulloides found in Pacific Grove, California. Laboratory observations of juvenile T. pulloides in a flow tank indicated that they are capable of producing mucous threads and drifting in a way similar to Lacuna spp.

Barleeia spp., Musculus sp. and Lasaea sp. belong to taxonomically complex groups. Several species of Barleeia occur in the northeast Pacific (Kozloff, 1983, 1987) Most adults collected in this study appear to be B. haliotiphila Carpenter, 1864 but could also include B. subtenuis Carpenter, 1864 and B. acuta Carpenter, 1864. Musculus sp.

Table 3.2

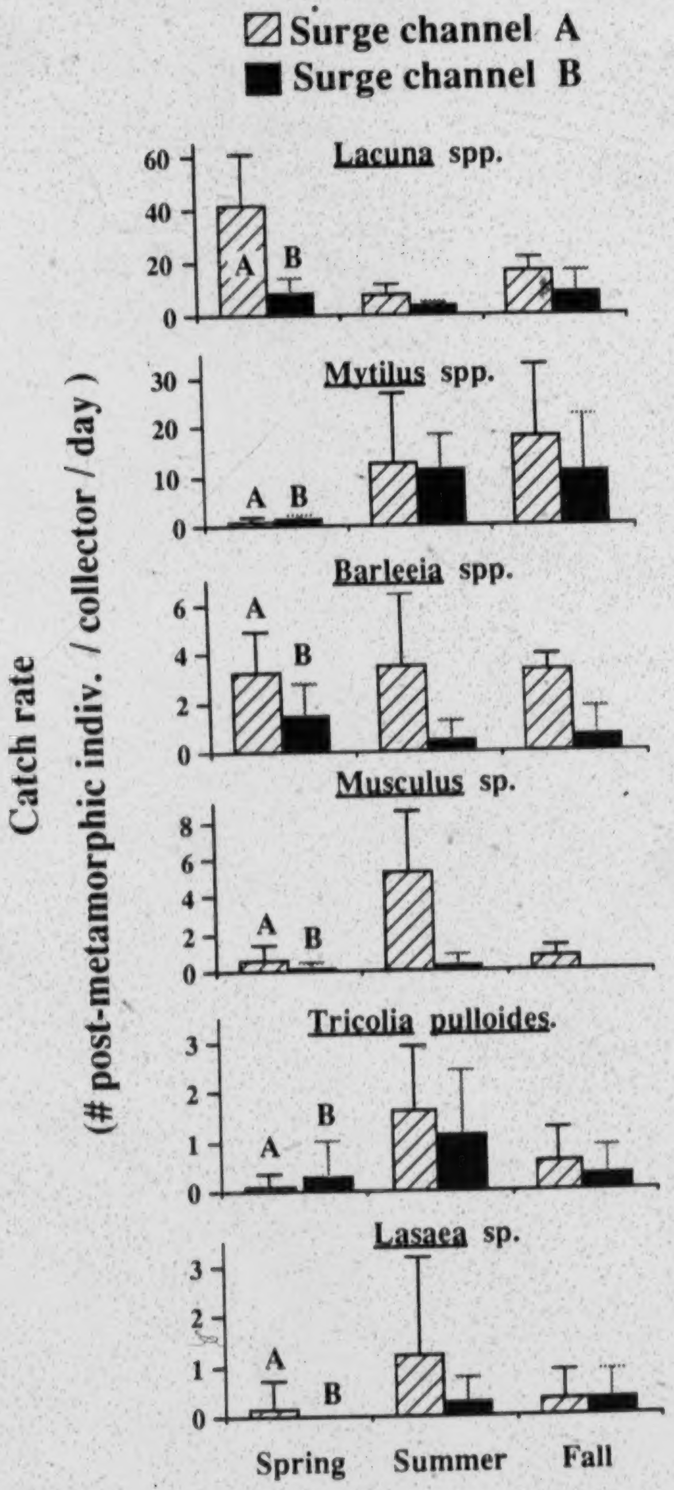
Seasonal abundance of post-metamorphic benthic invertebrates trapped in off-bottom intertidal collectors at Prasiola Point in 1988. List includes 18 taxa (17 molluscs and one echinoderm).

			Spring		Summer		Fall	
Type	Repro. mode	Taxa found in Collectors	Tot. (n)	Avg. Size (mm)	Tot. (n)	Avg. Size (mm)	Tot. (n)	Avg. Size (mm)
Ga	L	Lacuna spp	604	1.42	102	1.63	75	1.75
Bi	L	Mytilus spp	21	2.44	204	1.16	86	2.35
Ga	DE	Barleeia spp	52	1.34	38	1.38	12	1.02
Bi	DB	Musculus sp	8	0.92	55	0.73	2	2.18
1 Ga	?	Tricolia pulloides	3	2.40	24	0.79	3	1.77
Ga	L	Littorina scutulata	15	3.40	5	2.22	2	2.51
Ga	L	Limpet spp	4	3.29	14	0.93	3	1.36
Bi	DB	Lasaea sp	2	0.99	14	0.76	2	0.79
Bi	DB	Transennella tantilla	4	2.96	0		5	2.38
Bi	L	Hiatella artica	0		8	1.20	0	
Bi	L	Clam spp	4	0.47	2	0.68	0	
2 Ga	?	Alvania spp	2		1	1.19	1	1.23
As	DB	Leptasterias hexactis	3	0.69	0		0	
2 Ga	?	Margarites sp	0		3	3.05	0	
Ga	DE	Onchidella borealis	0		2	5.15	1	2.37
Ga	DE	Nucella emarginata	0		2	1.28	0	
Ga	DE	Littorina sitkana	1	3.17	0		1	2.30
Ga	L	Alia gouldi	1	7.92	0		0	

Type: Ga = gastropod, Bi = bivalve, As = asteroid

Reproductive mode:
L = With planktonic larval stage
DE = Direct development: egg capsules and crawl-away juv.
DB = Direct development: brooding
1 = Mooers (1981) reported direct development in *Tricolia pulloides* in Pacific Grove, California.
2 = Reproductive mode unknown

Figure 3.3. Abundances of six molluscan species in off-bottom intertidal collectors in the spring, summer and fall of 1988 at two different sites at Prasiola Point. Hatched bars: surge channel A; solid bars: surge channel B. Histograms show mean catch rates (# post-metamorphic ind./coll./day). Number of collector days (n) are, for surge channel A and B, respectively: spring: 13 and 7; summer: 10 and 7; fall: 3 and 3. Error bars represent ± SD.


▨ Surge channel A
■ Surge channel B
Catch rate
(# post-metamorphic indiv. / collector / day)
Lacuna spp.
60
40
20
0
A
B
Mytilus spp.
30
20
10
0
A
B
Barleeia spp.
6
4
2
0
A
B
Musculus sp.
8
6
4
2
0
A
B
Tricolia pulloides.
3
2
1
0
A
B
Lasaea sp.
3
2
1
0
A
B
Spring
Summer
Fall

found in the region of Vancouver Island could be *M. taylori* (Dall, 1897) (see Glynn, 1964). Many of the nominal *Lasaea* species, are, according to Ponder (1971), regional subspecies of *L. rubra* (Montagu, 1803). O'Foighil (1989) referred to them as "*Lasaea* species (undescribed)".

Sizes of juveniles and adults of the 4 most abundant species with direct development collected at Prasiola Point were: *Barleeia* spp., 0.42-0.43 mm and 2-3.5 mm; *Musculus* sp., 0.47-0.51 mm and 2-3 mm; *Lasaea* sp., 0.55-0.62 mm and 1.8-3 mm and *Transennella tantilla*, 0.52-0.55 mm and 2.5-4 mm. The proportion of juveniles to adults varied among the 4 taxa (Tables 3.1, 3.2). Most (84%) drifting *Musculus* sp. collected were small juveniles, with shell length < 1 mm (mean = 0.80 mm, SD = 0.41, *n* = 65) (Tables 3.1, 3.2). Up to 83% of the brooding bivalve *Lasaea* sp. collected had a shell length < 1 mm (mean = 0.79 mm). In contrast, although most *Musculus* sp. and *Lasaea* sp. individuals found drifting were small newly-released juveniles, most *T. tantilla* found in collectors were adults (1.8-3.9 mm); 5 out of the 9 individuals found were adults brooding embryos (Tables 3.1, 3.2). Also, 72% of the *Barleeia* spp. collected were large juveniles or sexually mature adults (length > 1 mm) (Fig. 3.2). Daily occurrence of these invertebrates in off-bottom collectors shows that, contrary to what their mode of development suggests, they are far from being sedentary.

Other species with direct development were found, but in low numbers (Tables 3.1, 3.2). Among them were three newly-released juveniles of the brooding asteroid *Leptasterias hexactis* (arm length: 0.61, 0.67 and 0.79 mm) caught drifting during early May (Fig. 3.2). This period also coincides with the release of brooded juvenile *L. hexactis* by adult females. A second species of echinoderm, the brooding sea cucumber *Cucumaria pseudocurata* (1 juvenile, length 1 cm), was also found in the collectors (summer of 1989) but was not included in tables. Finally, 2 newly-hatched juvenile neogastropods *Nucella emarginata* (shell length: 1.19 and 1.39 mm) were collected during the summer (July) when high numbers of juveniles emerged from their egg capsules (Fig. 3.2).

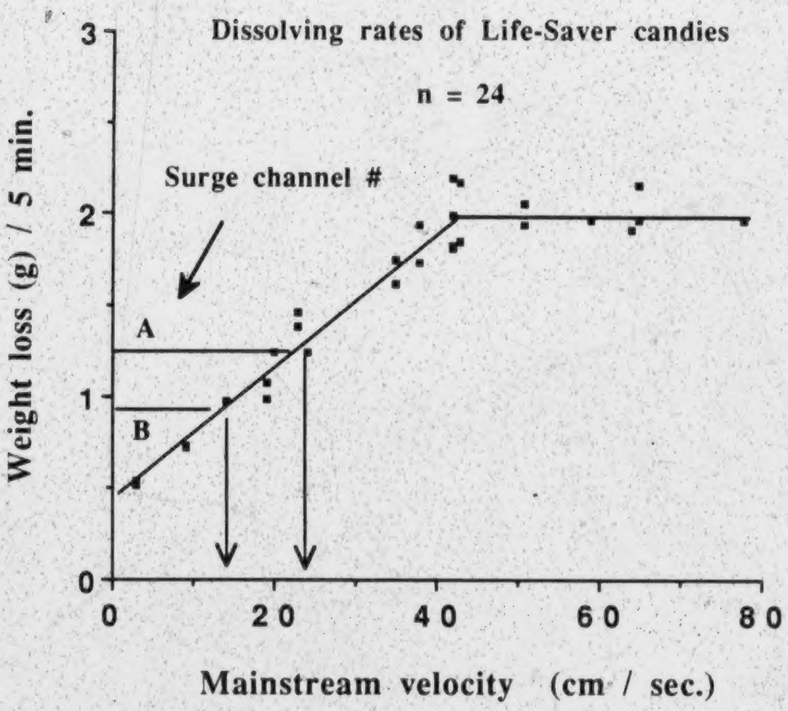
Two genera with long-lived planktonic larvae also found in the off-bottom intertidal collectors were juvenile *Lacuna* spp. (could include *L. vincta* and *L. variegata*) and *Mytilus* spp. (could include *M. edulis* and *M. californianus*) (Tables 3.1, 3.2; Figs. 3.2, 3.3). Measurements of protoconchs (*Lacuna* spp.) and prodissoconchs (*Mytilus* spp.) have enabled the determination of sizes of newly-metamorphosed individuals and the setting of a conservative limit for the determination of the stage (juvenile or larva) of individuals arriving at the collectors: juvenile *Lacuna* spp.: ≥ 1.00 mm; juvenile *Mytilus* spp.: ≥ 0.51 mm. (A. Martel, unpublished observations). The juveniles of these two species were the most abundant invertebrates collected. In surge channel A, during peak drifting periods, an average of 41.9 juvenile *Lacuna* spp. (in spring) and 18 juvenile *Mytilus* spp. (in fall) were found / collector / day (Fig. 3.3). It is also noteworthy to mention the presence of juvenile limpets in the water column ($n = 21$, average shell length = 1.44 mm) (Tables 3.1, 3.2).

2. Effects of hydrodynamic conditions, type of substratum and seasons on abundance of drifters in collectors

In situ dissolving rates of Life-Savers candies (peppermint) indicated significant differences in hydrodynamic conditions between the two surge channels studied (Fig. 3.4). Results showed that site A was subject to greater currents and surge than site B. The average weight loss of Life-Savers at site A was 1.2013 g / 5 min (SD = 0.0683 g, $n = 11$), compared with only 0.9774 g / 5 min (SD = 0.0547 g, $n = 8$) for site B (Kruskal-Wallis, $H = 13.20$, $p < 0.001$). In the laboratory, similar dissolution rates were obtained when a unidirectional flow was set at 14 and 24 cm / s, respectively (Fig. 3.4).

At the two study sites, the numbers of drifting animals differed significantly (Fig. 3.3). Although the two experimental areas were less than 100 m apart, higher numbers of *Barleeia* spp., *Musculus* sp. and *Lacuna* spp. were caught drifting at site A than at site B (Kruskal-Wallis, *Barleeia* spp., $H = 15.41$, $p < 0.001$, *Musculus* sp., $H = 8.92$, $p < 0.01$, and *Lacuna* spp., $H = 14.21$, $p < 0.001$) (Fig. 3.3). A similar trend is also suggested for *Lasaea* sp.. Differences in numbers of individuals found in collectors at each site could be related to local variations in population densities or in

Figure 3.4. Dissolving rates of Life-Savers candies (Peppermint) left for 5 minutes at different water velocities in a flow tank (10^o C). A and B represent mean *in situ* weight losses of similar Life-Savers left for the same period of time at high tide beside off-bottom collectors installed in two surge channels (A and B) at Prasiola Point on July 04, 1989.


Dissolving rates of Life-Saver candies
n = 24
Surge channel #
A
B
Weight loss (g) / 5 min.
0
1
2
3
0
20
40
60
80
Mainstream velocity (cm / sec.)

hydrodynamic conditions.

Abundance of individuals found in collectors at site A showed evidence of a seasonal pattern in Lacuna spp. (Kruskal-Wallis, $H = 19.37$, $p < 0.001$), Mytilus spp. ($H = 19.44$, $p < 0.001$), Musculus sp. ($H = 15.47$, $p < 0.001$) and Tricolia pulloides ($H = 12.87$, $p < 0.005$) (Fig. 3.3). High abundances of drifting juveniles of Lacuna spp., Mytilus spp. and T. pulloides correlated with main periods of recruitment (Martel, pers. obs.; see Mooers [1981] for breeding season of T. pulloides). As well, mussels and T. pulloides drifting during the summer were smaller than those collected during the spring (see Table 3.2). Increases in numbers of the clam Musculus sp. during the summer may have corresponded with the timing of release of juveniles from the adult brood chamber (Table 3.2; Fig. 3.3). Juveniles of other taxa such as limpets, Lasaea sp. and Hiatella arctica, also tended to be more abundant and smaller during the summer (Tables 3.1, 3.2, Fig. 3.3). The distribution of drifting juvenile and adult Barleeia spp. showed no apparent seasonal trend (Figs. 3.2, 3.3). It is noteworthy that patterns of abundance of the afore-mentioned drifting invertebrates coincide with periods of recruitment, rather than with prevailing average seasonal sea conditions (see Tables 3.1, 3.2).

Control collectors made of Kinran monofilament trapped and retained significantly fewer juvenile Lacuna spp. than did collectors made of the red alga Gracilaria pacifica (Table 3.3). Even though control Kinran collectors had 3

Table 3.3

Catch rate and size of *Lacuna* spp. and *Mytilus* spp. trapped in *Gracilaria* and Kinran intertidal collectors at Prasiola Point in June 1989. Mann-Whitney statistical test was used.

Catch rate		Density: # ind. /collector/day						
		Gracilaria			Kinran			
		Mean	SD	n	Mean	SD	n	p
Lacuna	Site A	10.60	3.209	5	2.00	1.000	5	< 0.02
Lacuna	Site B	6.33	3.777	6	1.49	0.509	6	< 0.01
Mytilus	Site A	5.00	5.958	5	2.40	2.073	5	> 0.05
Mytilus	Site B	0.83	1.329	6	1.83	1.834	6	> 0.05

Size		Shell length (mm)						
		Gracilaria			Kinran			
		Mean	SD	n	Mean	SD	n	p
Lacuna	Site A	1.53	0.591	5	1.79	0.715	5	> 0.05
Lacuna	Site B	1.49	0.509	6	1.50	0.984	6	> 0.05
Mytilus	Site A	0.67	0.204	5	0.66	0.119	5	> 0.05
Mytilus	Site B	0.67	0.027	6	0.66	0.096	6	> 0.05

times the surface area of those made of the red alga, five times fewer individual Lacuna spp. were collected per day in these collectors than in algal collectors (channel A: Mann-Whitney, $Z = -2.529$, $p < 0.02$; channel B: $Z = -2.617$, $p < 0.01$). There was, however, no significant difference between the number of juvenile Mytilus spp. collected in the two types of collectors for both surge channels (channel A: $Z = -0.212$, $p > 0.05$; channel B: $Z = 1.029$, $p > 0.05$) (Table 3.3).

There was also no significant difference between the average size of Lacuna spp. and Mytilus spp. trapped in Gracilaria and the Kinran collectors ($p > 0.05$; Table 3.3).

3. Drifting molluscs caught in offshore collectors

Three molluscan species with direct development were caught in Gracilaria collectors placed offshore, in the middle of the bay at First Beach, after only three trials of five days each: two Barleeia spp., two Lasaea sp. and one Musculus spp. (Table 3.4). Lasaea sp. and Musculus spp. trapped in offshore collectors were newly-released individuals, with shell length < 1 mm (Table 3.4). These results complement those obtained with intertidal collectors and clearly show that once drifting has been initiated, these invertebrates can leave the shore and disperse over considerable distances with their mucous or byssal threads. Similar to the results obtained with the intertidal collectors, juvenile Lacuna spp. and Mytilus spp. were by far the most abundant species found in the offshore collectors.

Table 3.4

List of post-metamorphic benthic invertebrates trapped in offshore collectors at Prasiola Point during the summer of 1989. Each trial represents 7 collectors left for 5 days.

Type	Repro. mode	Taxa found in Collectors	Number			Tot. (n)	Avg. Size (mm)	s.d. (mm)
			June 14-19	June 24-29	July 01-06			
Bi	L	*Mytilus* spp.	52	26	19	97	0.77	0.18
Ga	L	*Lacuna* spp.	10	5	8	23	1.29	0.26
Ga	DE	*Barleeia* spp.	1	0	1	2	1.96	0.14
Bi	DB	*Lasaea* sp.	1	0	1	2	0.95	0.50
Bi	DB	*Musculus* sp.	1	0	0	1	0.55	0

Type: Ga = gastropod, Bi = bivalve

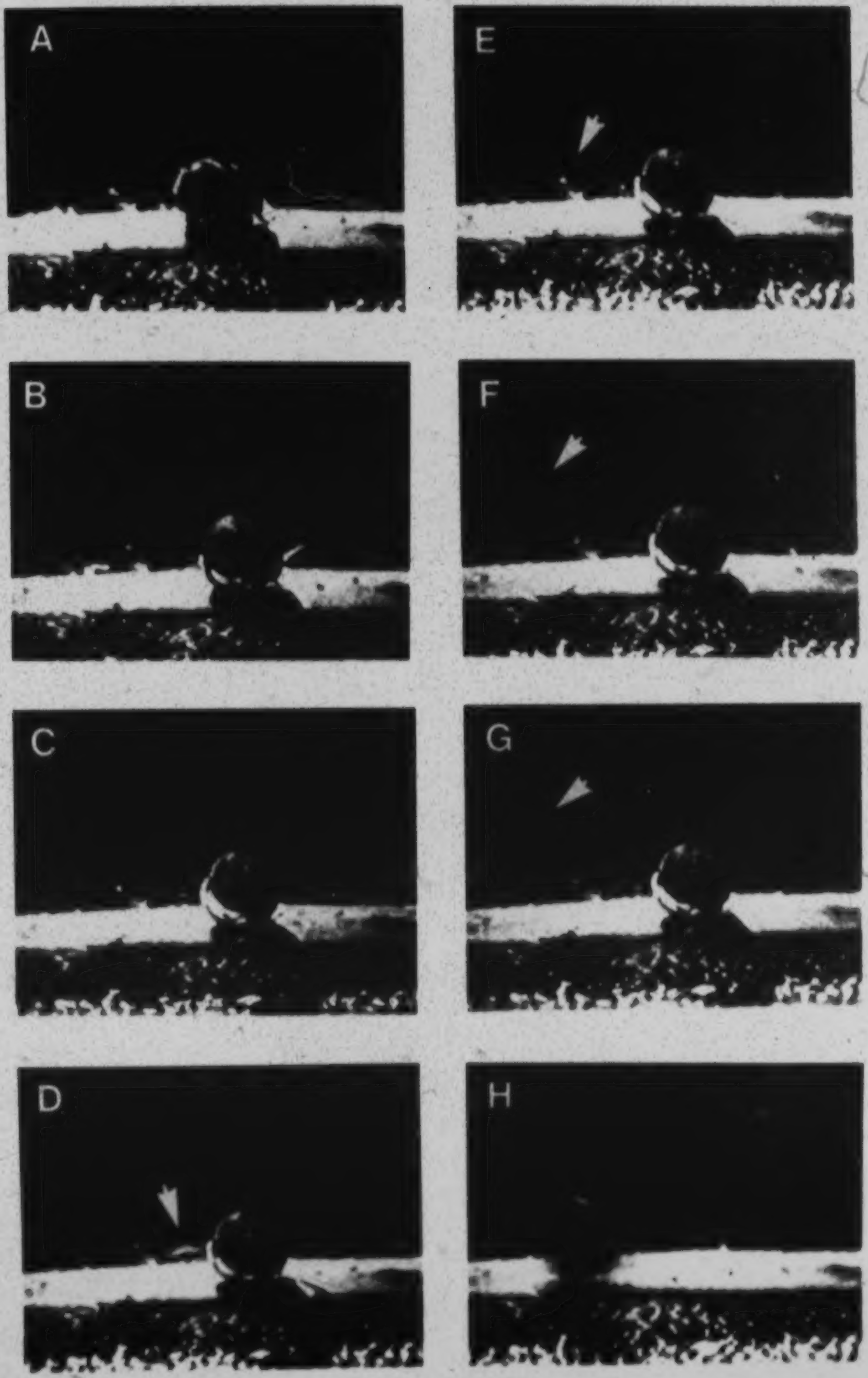
Reproductive mode:
L = With planktonic larval stage
DE = Direct development: egg capsules and crawl-away juv.
DB = Direct development: brooding

4. Production of mucous threads

a. Behaviour of Lacuna: mucous thread production

Macrocinematographic recordings of juvenile *Lacuna variegata* exposed to an oscillating flow similar to the surge observed in the intertidal zone have demonstrated that the production of a mucous thread and the initiation of drifting can be controlled by the animal. The series of photographs shown in Figure 3.5 shows a typical behavioural sequence during which a 2 mm juvenile *L. variegata* produces a long mucous thread before initiating drifting. The snail crawled and explored the seaweed for a few minutes; then it stopped and remained stationary for a few seconds. Facing the water flow, (anterior region toward current) (15-25 cm / s) the snail suddenly lifted the posterior part of its foot until this reached about 1/3 the height of the shell (Fig. 3.5 A, B, C). At that point, mucus produced and accumulated under the foot was carried by vortices downstream from the shell (Fig. 3.5 D, E, F) and rapidly stretched until it was no longer visible (Fig. 3.5 G). The drag created by mucus, coupled with the reduced tenacity of the snail as it lifted its foot, enabled the juvenile to take off quickly and initiate drifting (Fig. 3.5 H). This entire sequence lasted less than 1.6 seconds. Upon leaving the substratum, the snail drifted as if neutrally buoyant in the water column of the wave tank and was transported by the water turbulence for many minutes, until it came into contact with the side of the tank. This behaviour was repeatedly recorded on video tapes.

Figure 3.5. Photographs taken from a video sequence showing a juvenile Lacuna variegata (2 mm shell length) producing a mucous thread and initiating drifting in a surge tank. Water flow originated from the right at 15-25 cm / s. A) Prior to the raising of the foot. B-C) Raising of the posterior part of the foot. D-G) Release and stretching of the mucus from under the posterior part of the foot (see arrows); note that the mucous thread becomes less visible as the stretching process takes place. H) Snail pulled by its mucous thread initiates drifting. The duration of the entire sequence is 1.6 s.


A
B
C
D
E
F
G
H

The series of photographs shown in Figure 3.6 represents another video sequence that clearly shows how the snail raises the rear part of its foot to initiate drifting. Contrary to the first sequence, the snail in Figure 3.6 initiates drifting while the water flow comes from the posterior region of the animal. It was noticed that the behavioural pattern remained the same -- the posterior part of its foot was lifted -- even though the water flow was from the opposite direction. In this behavioural sequence, it is clear that the concave shape of the sole at the time the foot is raised reduces the surface contact between the animal and the substratum. This is an indication that the snail voluntarily releases itself from the substratum. These observations, coupled with laboratory experiments that snails exposed to water flow as high as 70 cm / s were not dislodged, confirm that in Lacuna spp. foot raising behaviour and drifting are initiated by the animal. In addition, this behaviour was more frequently displayed when snails were exposed to oscillating rather than unidirectional water flows.

The ability of snails to produce a copious amount of mucus that can be stretched by water currents to produce a drifting thread is shown in Table 3.5. When juvenile and adult Lacuna vincta, L. variegata and Barleeia spp. (the most abundant snails found in collectors) were placed individually in a small dish and gently spun in a circle for a few seconds, a mucous thread was produced 85-100% of the time

Figure 3.6. Photographs taken from a video sequence showing a juvenile Lacuna variegata (2.5 mm shell length) raising the posterior part of its foot prior to initiating drifting. A mucous thread, not visible in the pictures, was produced. Flow originates from the right at 15-25 cm / s. Note the height reached and the concave shape of the foot sole which reduces the surface contact between the foot and the substratum. The snail initiates drifting and move towards the left, carried by the water flow, even though picture H gives the contrary impression (picture framing problem). The duration of the entire sequence is 3.5 s.

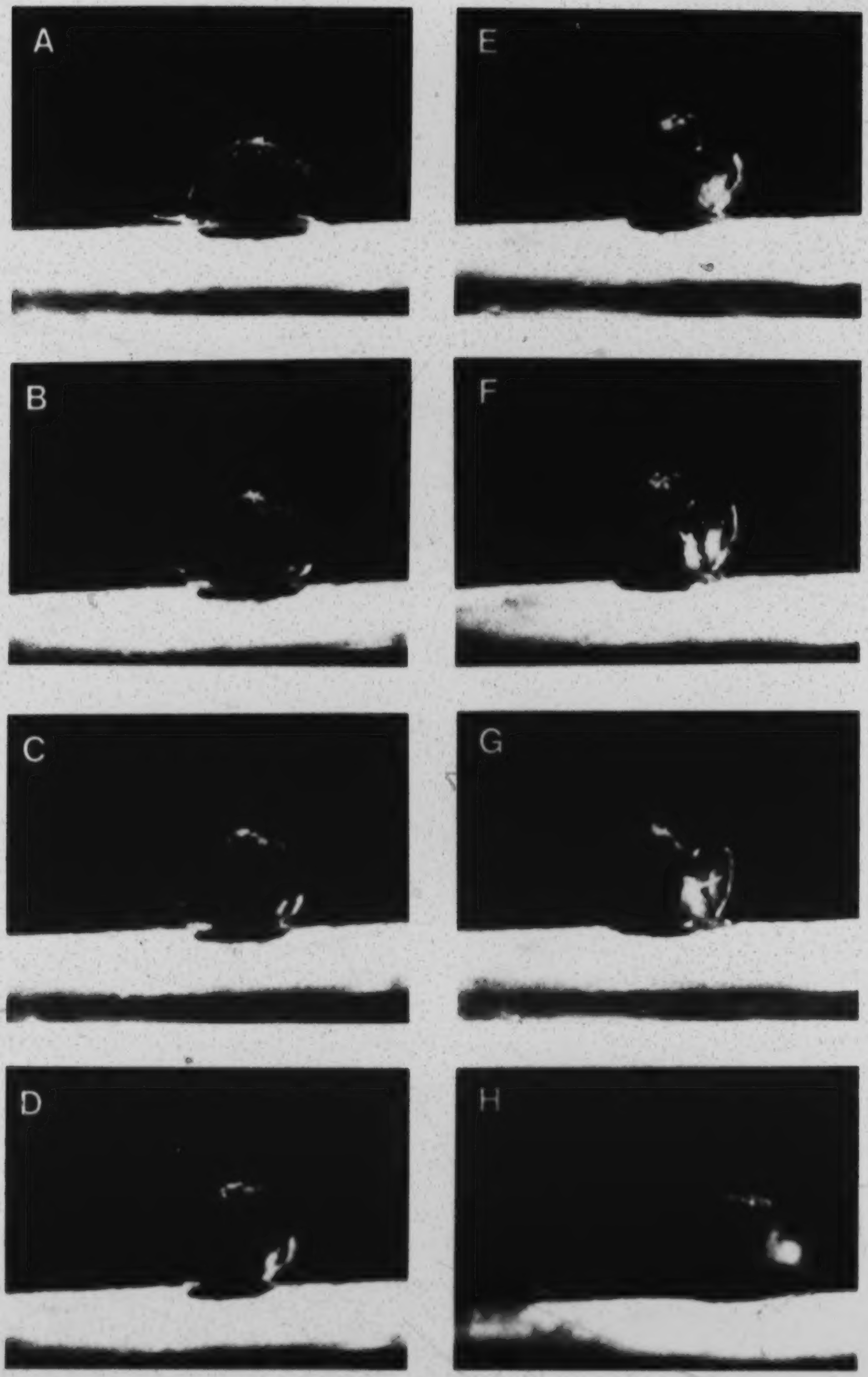

A
B
C
D
E
F
G
H

Table 3.5

Ability of five gastropods to produce a mucous thread when spun in a small glass dish. Numerators indicate number of times the animals produced a thread seizable with forceps; denominators indicate number of animals tested. Same animals were used for the three trials.

Species	Trials # 1	2	3
Lacuna variegata	14/14	13/14	12/14
Lacuna vincta	17/18	18/18	18/18
Barleeia spp.	14/15	15/15	15/15
Alia gouldi	1/12	1/12	1/12
Nucella emarginata	0/9	0/9	0/9

(confirmed by pulling the animal with a pair of forceps placed a few cm behind it). These results markedly contrast with those obtained when using individual Nucella emarginata (1.5-3 mm) and Alia gouldi (7-11 mm) -- two of the least abundant gastropod species found in the collectors -- for the same experiment (Table 3.5). This suggests that the latter two gastropods don't usually produce a mucous thread for drifting.

b. Length of mucous threads released by Lacuna vincta

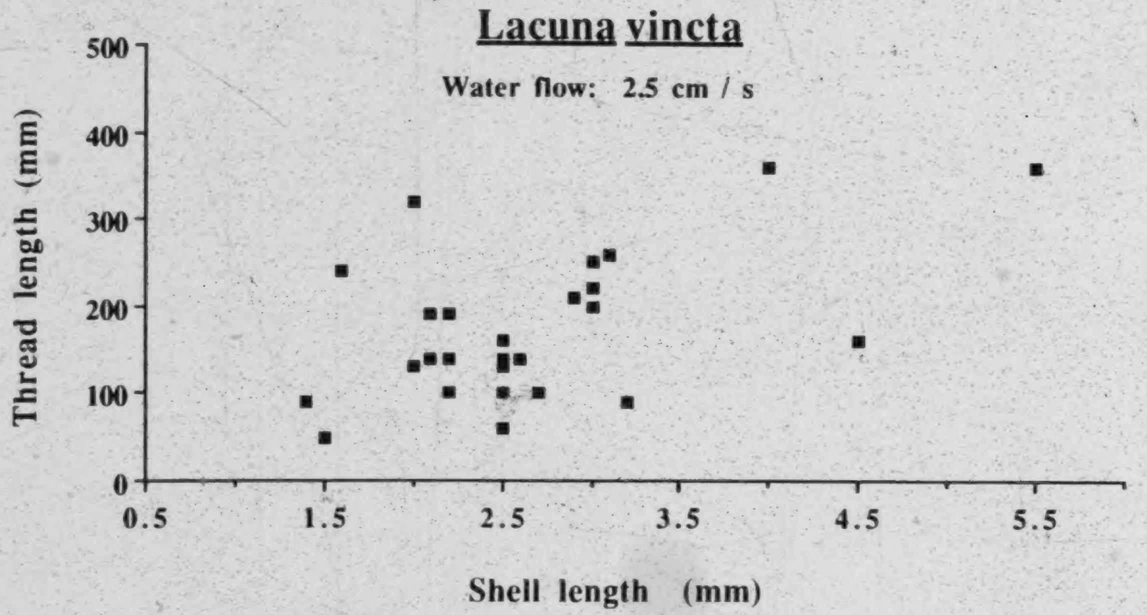
Experiments in a flow tank indicated that the mucous thread produced by Lacuna vincta during drifting can be surprisingly long (Figs. 3.7, 3.8). In small juveniles, the length of the mucous thread before rupturing can be 50-150 times the length of the shell. For example, one juvenile L. vincta of 2 mm shell length had a thread 320 mm long, 160 times the length of the shell (Fig. 3.7). Large juveniles and adults tended to produce longer threads and there was a significant correlation between thread length and the size of the snail ($r = 0.52$, $p < 0.05$).

5. Effects of mucus on snail sinking rates

a. Lacuna spp.

The presence of a mucous thread greatly reduced sinking rates of snails (Fig. 3.9). For juvenile Lacuna variegata of 1.25-2.25 mm shell length, sinking rates were on average 3.63 times lower when snails produced a mucous thread compared with those that did not (with thread: mean = 1.889 cm / s, SD

Figure 3.7. Relationship between the length of the mucous thread and shell length in _Lacuna vincta_. Experiments conducted in a flow tank (2.5 cm / s). Each point represents length of mucous thread measured at the point of rupture; $r = 0.52$, $p < 0.05$.



Lacuna vincta

Water flow: 2.5 cm / s

Figure 3.8. Photograph taken from a video sequence showing a drifting adult Lacuna vincta (6 mm shell length) and its mucous thread. The thread (17-20 cm long) can be seen because of the numerous detritus particles trapped on it reflecting the light. The snail appears as a large white spot at the bottom left corner of the picture.

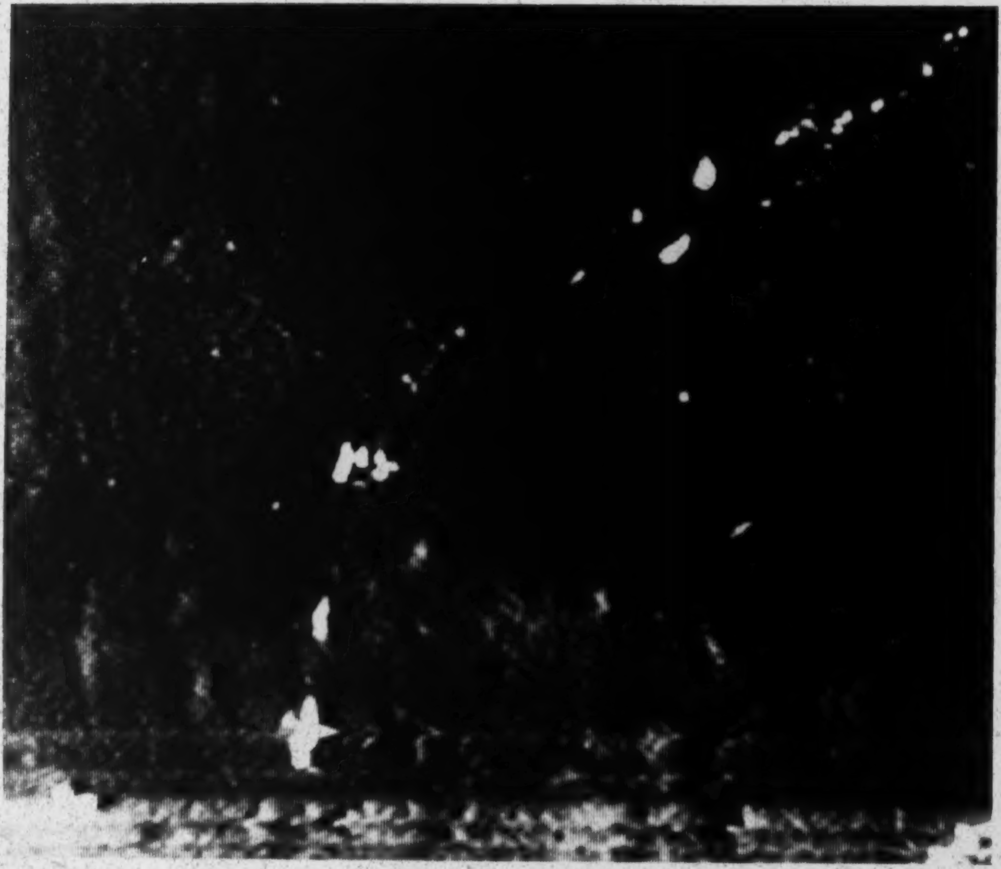
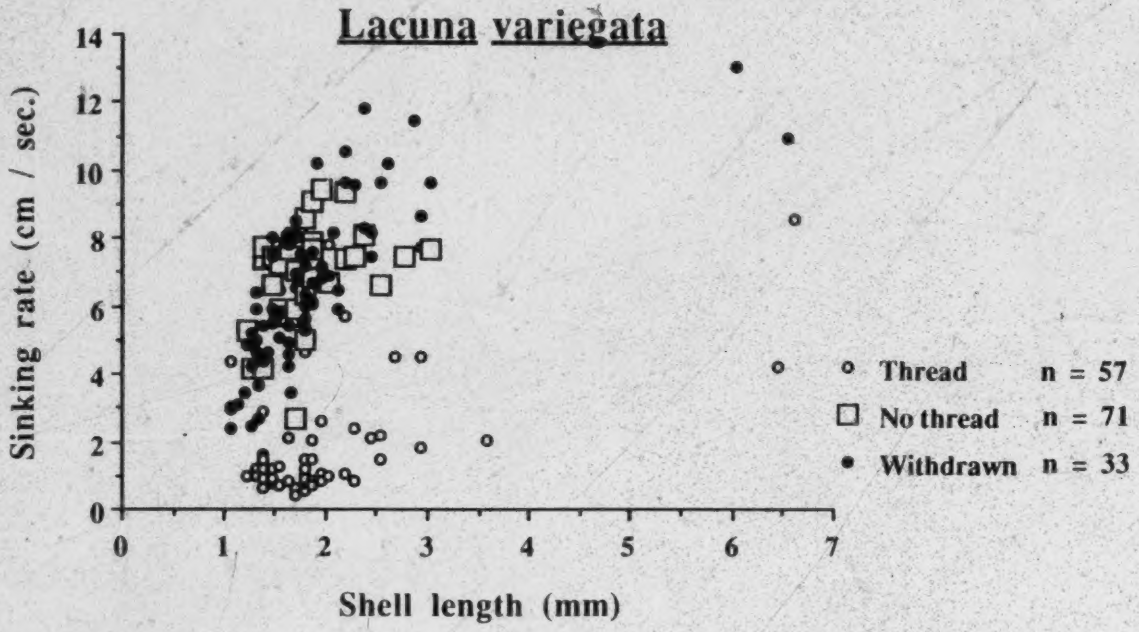


Figure 3.9. Sinking rates of Lacuna variegata in three behavioural situations: 1) snail with mucous thread, 2) snail without mucous thread, and 3) snail withdrawn into shell.


Lacuna variegata
Sinking rate (cm / sec.)
0
2
4
6
8
10
12
14
Shell length (mm)
0
1
2
3
4
5
6
7
○ Thread n = 57
☐ No thread n = 71
● Withdrawn n = 33

= 1.898, n = 41; without thread: mean = 6.861 cm / s, SD = 1.588, n = 27) (One-way ANOVA, F = 90.69 , $p < 0.001$) (Fig. 3.9). Similar observations were made with L. vincta. Also, the extension of the foot and antennae during descent did not significantly reduce sinking rates of snails (ANCOVA, differences among slopes and among means: $p > 0.05$). Large juvenile and adult Lacuna spp. were also capable of significantly reducing their sinking rates by using mucous (Fig. 3.9). Laboratory experiments showed that, given sufficient water current and turbulence, adults are capable of drifting and remaining in the water column for extended periods of time (Fig. 3.8). They require, however, greater upward flows to remain in suspension and are not as efficient at drifting as juveniles $\leq$ 2 mm (shell length) (Fig. 3.9).

b. Other gastropods

Neither Nucella emarginata nor Littorina sitkana are recognized as good drifters (see Tables 3.1, 3.2, 3.5). Experiments on sinking rates indicated that individuals $\geq$ 2 mm shell length sank in the water column following a power function of the type $y = ax^n$ (y = sinking rate; x = shell length), where $0 < n < 1$ (Figs. 3.10 A, 3.11 A). Mucus did not appear to play any significant role in sinking rates of these large individuals.

Unexpected results were obtained, however, when studying sinking rates of juveniles < 1.5 mm (Figs. 3.10 B, 3.11 B). Newly-hatched juvenile Nucella emarginata of 1.0-1.4 mm shell length that were manually dislodged from their substratum

Figure 3.10. Sinking rates of Nucella emarginata. A) Sinking rates of snails from newly-hatched to adult sizes. B) Enlarged portion of the graph shown in A, showing sinking rates of newly-hatched juveniles (0.92-2.00 mm) in three behavioural situations: 1) snail with mucous thread, 2) snail without mucous thread, and 3) snail withdrawn into shell.

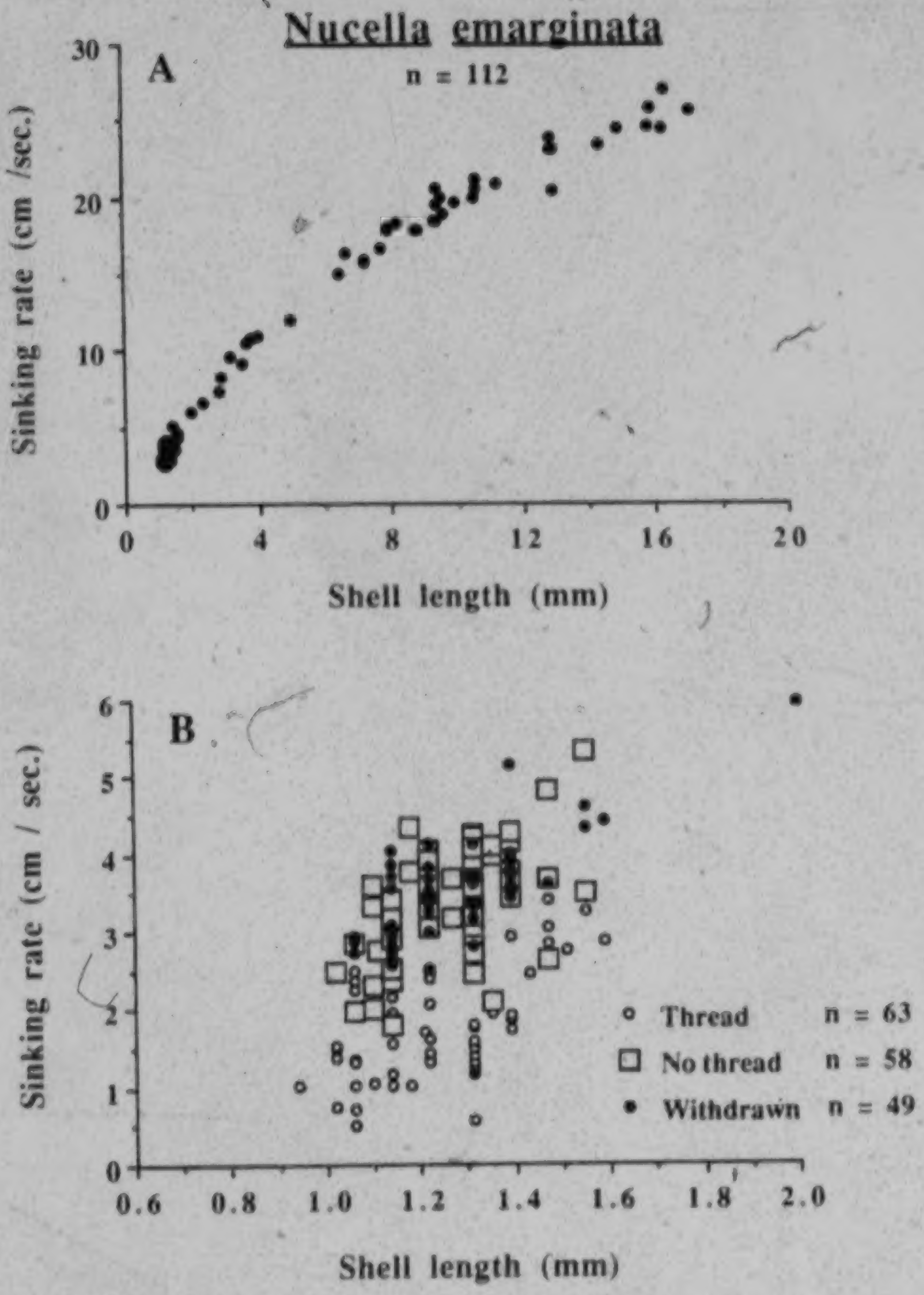
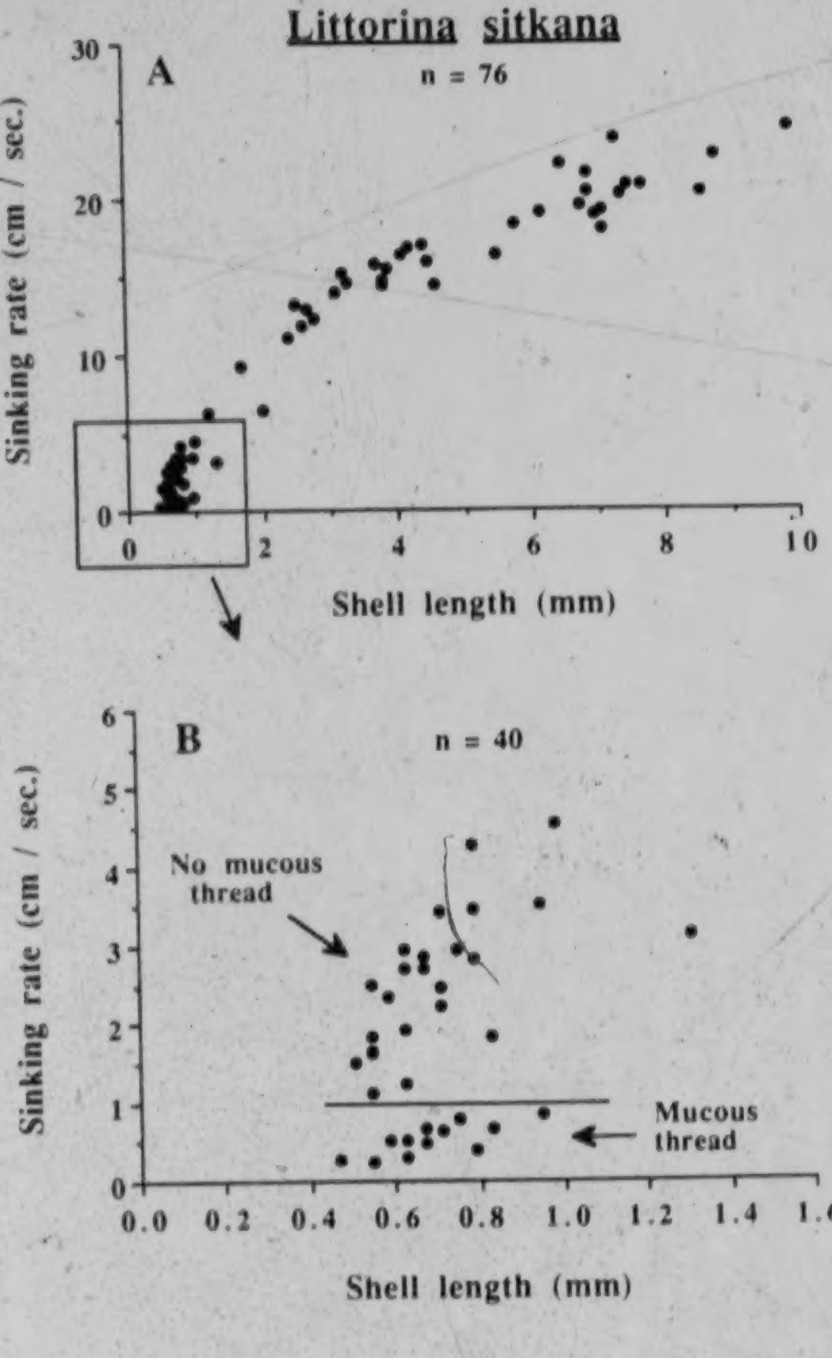

Nucella emarginata
A
n = 112
Sinking rate (cm /sec.)
0
10
20
30
0
4
8
12
16
20
Shell length (mm)
B
Sinking rate (cm / sec.)
0
1
2
3
4
5
6
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Shell length (mm)
○ Thread n = 63
□ No thread n = 58
● Withdrawn n = 49

Figure 3.11. Sinking rates of *Littorina sitkana*. A) Sinking rates of snails from newly-hatched to adult sizes. B) Enlarged portion of the graph in A, showing sinking rates of newly-hatched juveniles. Lowest sinking rates (< 1 cm / s) were achieved only when individuals had produced a mucous thread.

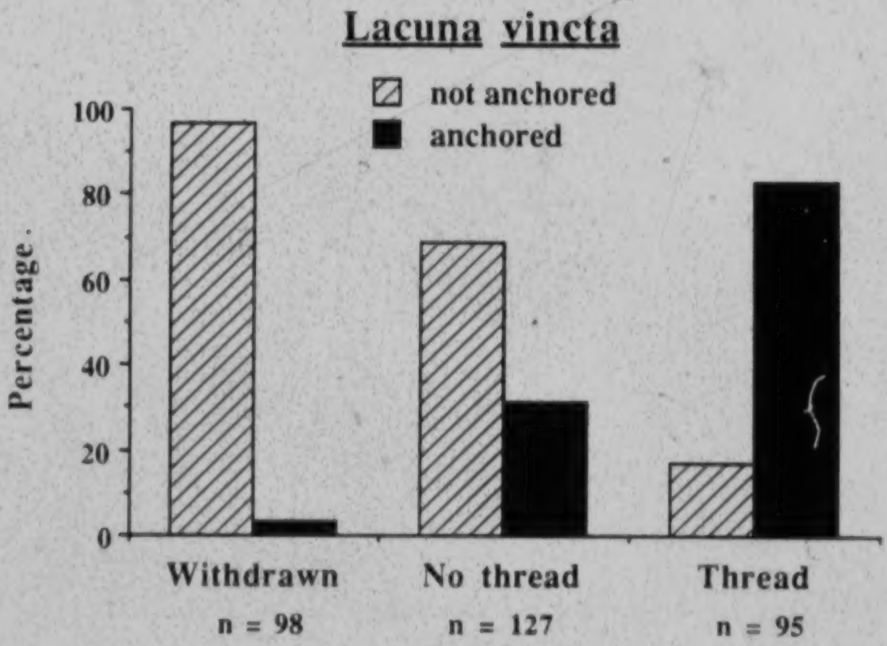

Littorina sitkana
A
n = 76
Sinking rate (cm / sec.)
30
20
10
0
0
2
4
6
8
10
Shell length (mm)
B
n = 40
Sinking rate (cm / sec.)
6
5
4
3
2
1
0
No mucous thread
Mucous thread
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Shell length (mm)

sank at different speeds depending on whether or not they had produced a mucous thread (with thread: mean = 1.915 cm / s, SD = 0.797, n = 63; without thread: mean = 3.396 cm / s, SD = 0.711, n = 58) (One-way ANOVA, F = 55.67, p < 0.001) (Fig. 3.10 B). Protruding foot and antennae without producing a mucous thread did not significantly reduce sinking rates of juvenile (1.0-1.4 mm) N. emarginata (ANCOVA, differences among slopes and means, p > 0.05) (Fig. 3.10 B). Similar results were obtained with newly-hatched juvenile Littorina sitkana of 0.5-1.0 mm shell length (Fig. 3.11 B), where many individuals that produced a mucous thread sank at rates as low as 0.25-0.50 cm / s. These sinking rates were 3-6 times lower than those of individuals that did not produced a thread (Fig. 3.11 B). Thus, these results show that because of their small size and the important drag created by the mucous thread, newly-hatched juvenile L. sitkana and N. emarginata have the ability to reduce their sinking rates significantly when dislodged.

6. The use of mucous threads in attachment to substratum

The presence of a mucous thread greatly helped drifting Lacuna vincta to attach to a substratum (Fig. 3.12). As many as 83.2% of the L. vincta with mucous threads became attached to the screen as they passed though the holes, compared to only 31.5% of snails without threads (G-test, G(W) = 153.12, p < 0.001) (Fig. 3.12). This ratio is conservative because it was not always possible to eliminate the production of a

Figure 3.12. Percentage of adult Lacuna vincta capable of attaching to a substratum while drifting in the water column during three behavioural situations: 1) snail with mucous thread, 2) snail without mucous thread, and 3) snail withdrawn into shell.

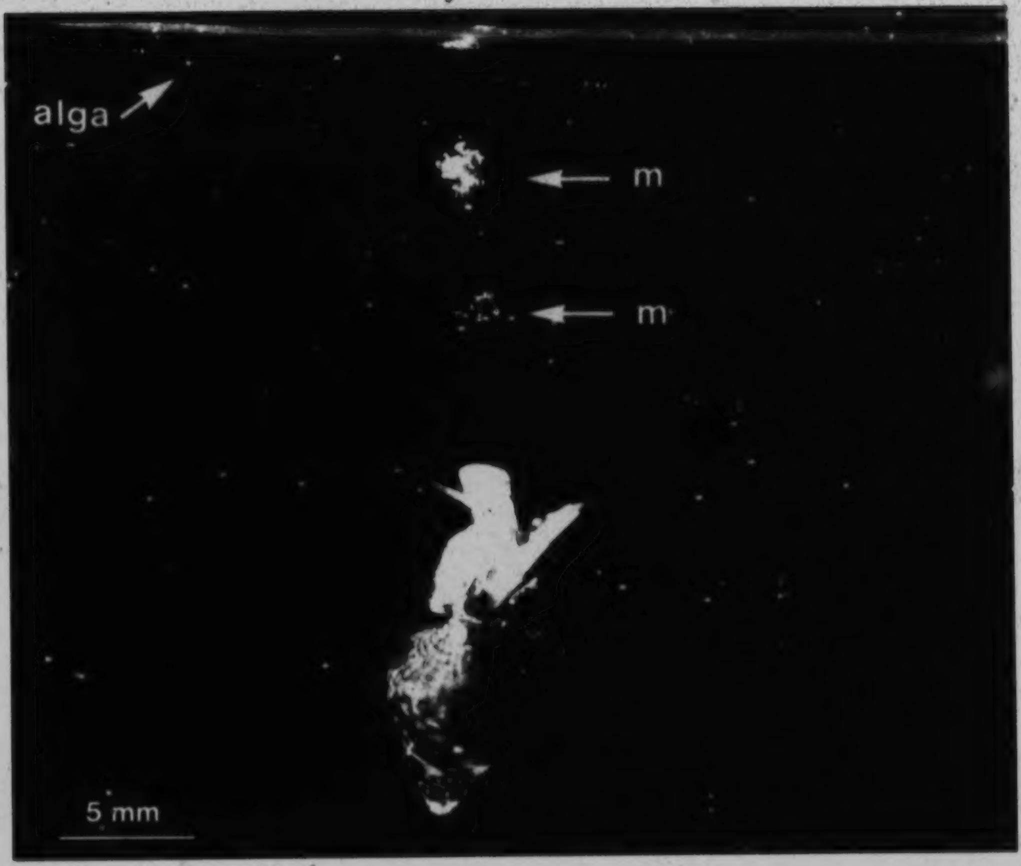

Lacuna vincta
▨ not anchored
■ anchored
Percentage
100
80
60
40
20
0
Withdrawn
n = 98
No thread
n = 127
Thread
n = 95

mucous thread in snails dropped when holding the sides of the shell with forceps. The value of 3.1% obtained with the control (withdrawn) snails is explained by the occurrence of a few individuals that rapidly came out of their shell during their descent and successfully attached to the screen with their sticky foot as they went through. The difference in the proportion of snails that were successful in catching the substratum is significant between all subsets (R X C, G-test, $p < 0.001$; see Sokal and Rohlf, 1981).

7. Role of mucous threads in a non-drifting snail: *Alia gouldi*

The small neogastropod *Alia gouldi* (adult shell length: 9-14 mm) is common on seaweeds and eelgrass in low intertidal and shallow subtidal areas. Observations conducted during SCUBA diving in subtidal *Zostera marina* beds revealed that *A. gouldi* can produce a strong mucous thread that is used as an anchor line rather than for drifting (Fig. 3.13). Adult *A. gouldi* were observed hanging at the end of their thread (up to 10-20 cm long). By seizing the thread with its foot, even an adult snail is capable of climbing back up to the blade to which the thread was attached. While crawling, *A. gouldi* appeared continuously to produce a mucous thread, and regularly fixed "mucous pads" onto the substratum (Fig. 3.13). Observations of these snails on their threads suggested that these mucous pads represented a safety mechanism preventing a dislodged animal from falling off the

Figure 3.13. Adult Alia gouldi (11 mm shell length) hanging from and climbing back up its mucous thread which remained attached to a blade of an alga. Note the mucous pads (m) indicated by arrows.


alga
m
m
5 mm

plant.

The production of mucous threads by Alia gouldi was not induced as it was with Lacuna spp. or Barleeia (Table 3.5), and observations of live animals under the dissecting microscope revealed that the mechanism by which its mucous thread is produced differs from that of Lacuna spp.. Mucous threads produced by A. gouldi come primarily from two specialized ciliated grooves that run on each side of the foot, between the head area and the operculum. In each of these grooves, the mucus is carried, as if on a conveyer belt, toward the posterior of the animal. The two mucous strings, one from each side, follow the grooves and meet just behind the operculum, where they unite to form the thread.

8. Structure of mucous threads

a. Mucous threads used by drifters: Lacuna spp. and Barleeia spp.

The examination of the mucous thread of Lacuna vincta and Barleeia spp. under phase contrast and scanning electron microscopes revealed high numbers of parallel fibers that run along the entire length of the threads (Figs. 3.14, 3.15). Wet mount preparations showed wide variations in thread diameters, ranging from ± 5 µm to 40 µm (Fig. 3.14). Such wide variations in diameters, and the rupture of many fibers at the periphery of the thread, may be due to the different degrees of stretching that occur during drifting as well as during wet mount preparation. In addition, the thread may be

Figure 3.14. Photomicrographs of Lacuna vincta's and Barleeia's drifting mucous threads taken with a phase contrast microscope. A, B, C) Lacuna vincta. D) Barleeia spp.. Bars represent 7 µm. Note the parallel fibers in the four photographs.

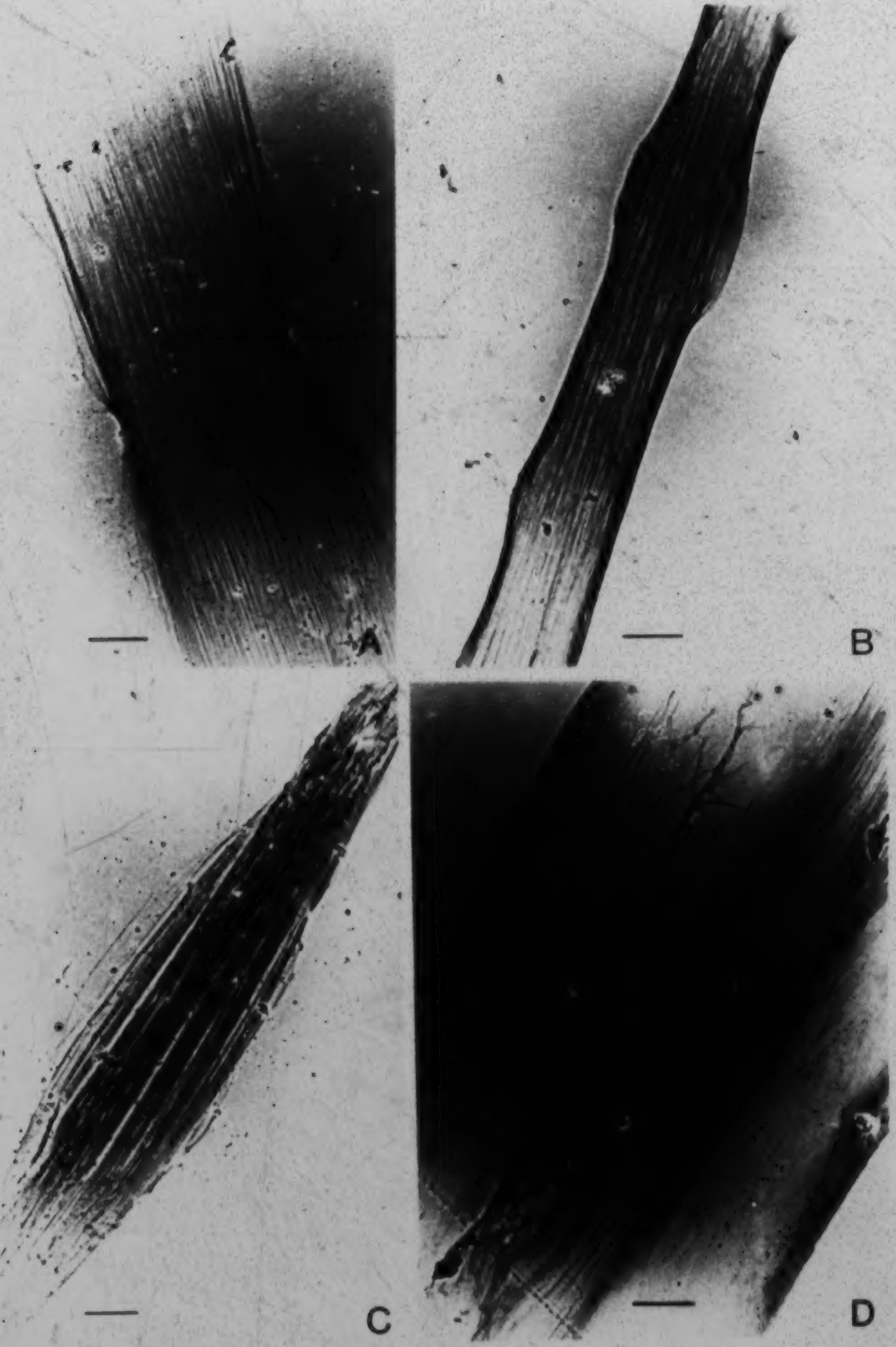
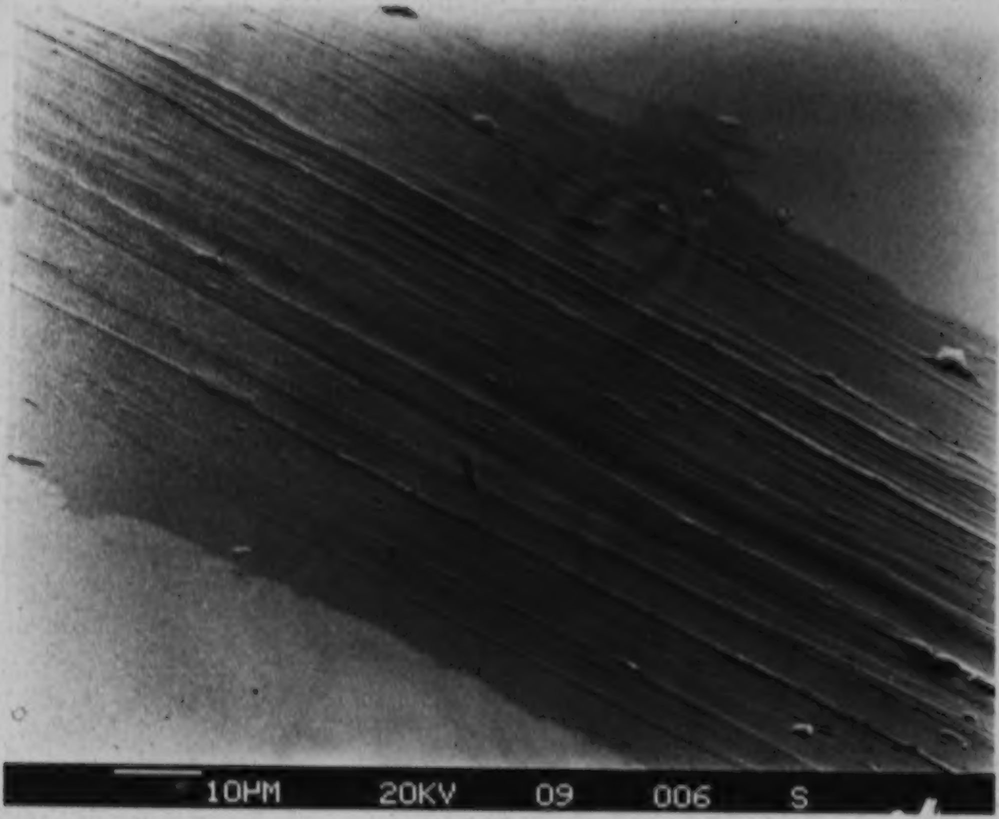

A
B
C
D

Figure 3.15. Photomicrograph of Lacuna vincta's mucous thread taken with a scanning electron microscope. Note the parallel fibers. The large diameter of the thread could be due to deformation occurring during mounting and preparation.


10µM
20KV
09
006
S

deformed when it is washed with freshwater, air dried or as the cover slip is placed over it.

b. Mucous thread used by a non-drifter: *Alia gouldi*

The structure of the stronger mucous thread of the non-drifting *Alia gouldi* is more complex (Figs. 3.16, 3.17). Most striking is the presence of more than just one type of fiber and the way they are coiled together, similar to a rope (Fig. 3.16). Representing the bulk of *A. gouldi*'s thread is an inner core of numerous parallel fibers that coil together as they progress along the thread (Fig. 3.16 A). The second component of the mucous thread resembles a monofilament fiber surrounding or wrapping the inner core (Fig. 3.16 B). This outer fiber appears twisted around the inner fibers, with the number of turns per unit of distance (pitch) being much higher than that of the inner core fibers. *A. gouldi*'s mucous thread also showed wide variations in diameter, ranging from ± 4 to 25 µm (wet mount preparations).

D. DISCUSSION

Post-metamorphic drifting plays an important role in the life history of many benthic marine invertebrates, especially small molluscs living on intertidal seaweed. For certain species that lack a free-swimming planktonic larval stage, post-metamorphic drifting constitutes an alternative mechanism for dispersal and recruitment. Results from the present study also show that drifting, at least in *Lacuna* spp., can be initiated by the animal. In addition, the

Figure 3.16. Photomicrographs of Alia gouldi's attachment mucous thread taken with a phase contrast microscope. The pictures show two distinct coiled fiber components of the thread. The thread diameter is 5-7 um.
A) Focus on the low pitch fibers (see center of picture).
B) Focus on the high pitch fibers.

A
B

Figure 3.17. Photomicrograph of Alia gouldi's attachment mucous thread taken with a scanning electron microscope. Note the coiling of the low pitch fibers (high pitch fibers are not visible on the picture).

4µM
20KV
06
010
S

morphology of the mucous threads produced by drifting gastropods markedly differs from that of threads produced by non-drifters.

1. Widespread phenomenon of post-metamorphic drifting

Results obtained with off-bottom collectors placed in semi-exposed rocky intertidal and nearshore areas demonstrated that several marine benthic invertebrates lacking a planktonic larval stage are commonly found in the water column and can rapidly disperse locally by drifting. Among the ten most common benthic marine invertebrate taxa found drifting and caught in off-bottom collectors are the small prosobranch gastropod *Barleeia* spp., all known species of which produce benthic egg capsules with crawl-away juveniles (Ponder, 1983), and three brooding bivalves: *Musculus* sp., *Lasaea* sp. and *Transennella tantilla*. Three of these taxa (*Barleeia* spp., *Musculus* sp. and *Lasaea* sp.) have also been found in collectors placed away from the shore in deeper waters. The regular occurrence of these taxa in the water column thus contradicts the assumption that these organisms are essentially sedentary and have reduced dispersal capabilities. These taxa are also known to have wide geographical ranges (see Abbott, 1974; Morris *et al*., 1980); for example, the brooding bivalve *Lasaea* sp. has a near-cosmopolitan distribution (Ponder, 1971; Beauchamp, 1986; O'Foighil, 1989), including many remote oceanic islands world-wide (see O'Foighil, 1989).

Several authors have reported finding brooding bivalves in the water column, just above the sediments (e.g. the clam Gemma, Sullivan, 1948; Sellmer, 1967). Prezant and Charlermwat (1984) demonstrated the ability of the brooding fresh water clam Corbicula fluminea to produce long mucous threads which suspend the animal in the water column. In addition, Booth (1979) reported the occasional presence of Lasaea rubra in plankton tows.

Several authors have expressed difficulty in explaining how bivalves that incubate low numbers of non-swimming young achieve such widespread distributions (see Highsmith, 1985; Beauchamp, 1986). Rafting is believed to be the most probable alternate method of long range dispersal in many brooding invertebrates (e.g. Dell, 1972; Highsmith, 1985; also see Jackson, 1986). O'Foighil (1989) reported that the brooder Lasaea sp. has a much greater geographical distribution than its sibling, Lasaea australis, which has a free-swimming planktonic larval stage. He suggested that rafting was the mechanism by which Lasaea sp. disperses. Johannesson (1988) reported a similar situation in two species of intertidal gastropods, mentioning that Littorina saxatilis, which broods its embryos to the crawl-away juvenile stage, has a much more widespread geographical distribution than the closely related L. littorea. Johannesson suggested that in L. saxatilis, adults, juveniles, or benthic egg masses can drift over long distances and colonize new habitats. He hypothesized that transport of benthic stages could be more influential than larval dispersal over long distances. Moreover, in a study on Antarctic benthos, Dell (1972) speculated that a brooding female invertebrate is a better colonist than a larva. Frequent excursions in the water column, coupled with the presence of byssal or mucous threads, may increase the animal's chances of encountering floating or rafting objects while drifting which, in turn, could greatly enhance chances of long distance dispersal (see Arnaud et al., 1976; Highsmith, 1985; Jackson, 1986).

Laboratory observations indicated that newly-emerged Nucella emarginata are capable of producing a mucous thread when dislodged. The presence of two of these juveniles in the collectors at Prasiola Point during the summer suggests that they are capable of drifting in the water column. Moore (1938) speculated that newly-released juvenile Purpura (=Nucella) lapillus were capable of migrating from the high intertidal -- where egg capsules had been deposited -- to the low intertidal feeding area and that this migration was probably accomplished by juveniles drifting with wave action.

The presence of three newly-released individuals of the brooding seastar Leptasterias hexactis in the off-bottom collectors is of particular interest because they were collected at the time when most females release their juveniles (April-May; Ricketts et al., 1985). It is possible that some newly-released juvenile L. hexactis from each brood may disperse in the water column with surge. I have not however, noticed any evidence of copious mucous production by these juvenile seastars.

The branchy red alga Gracilaria pacifica employed for making the collectors was likely not the most effective material for collecting or attracting juvenile rock dwellers such as Leptasterias hexactis and Nucella emarginata. Collectors made of materials such as barnacle-covered rocks or pebbles (to serve as food for juveniles), may have retained more drifting invertebrates. The presence of only a few individuals of these two species in off-bottom collectors, although indicative of drifting, is not sufficient to assess clearly the significance of juvenile drifting in these two species. More research is thus needed.

In the present study, several species of gastropods and bivalves with long-lived planktonic larvae have been found drifting and caught in large numbers in the collectors. These include the gastropod Lacuna spp. and the mussel Mytilus spp., which were, by far, the two most abundant drifters. Post-metamorphic drifting has been reported in Lacuna spp. and Mytilus (Lacuna: Johnson and Mann, 1986; Martel, 1987, 1988; see Chapter II, IV; Mytilus: Bayne, 1964; Sigurdsson et al., 1976; de Block and Tan-Maas, 1977; Lane et al., 1982, 1985) as well as in other gastropod and bivalve species (gastropods: Sigurdsson, 1980; Vahl, 1983; Martel, 1988; bivalves: Bayne, 1964; Sigurdsson et al., 1976; Sigurdsson, 1980; Prezant and Charlermwat, 1984; Martel, 1988; Beukema and de Vlas, 1989).

Certain life history characteristics of several species lacking a planktonic larval stage and commonly found drifting contribute to effective colonizing strategies. Two of these characteristics, simultaneous hermaphroditism and self-fertilization, are found in the genus Lasaea (Crisp et al., 1983; O'Foighil, 1987; O'Foighil and Eernisse, 1988) and enable a single drifting individual to colonize a new area. In addition, filter-feeding can be an adaptive advantage during long distance dispersal. Also, the ability of many gastropods to store sperm after copulation, often for extended periods of time, could mean that a drifting female Barleeia spp. (adult size < 4 mm) is able to deposit capsules containing fertilized eggs once settled in a new area. With these mechanisms, the chances of a drifting (or rafting) Barleeia spp. or Lasaea sp. colonizing a new area are probably much greater than those of a single drifting planktonic larva (see Dell, 1972; Johannesson, 1988; O'Foighil, 1989).

Dispersal not only allows species to maintain existing populations but also enables them to escape adverse local conditions and colonize new areas. It is generally assumed that benthic marine invertebrates whose life history does not include a free-swimming planktonic larval stage will have, as a result, a more restricted geographic range than those with a free-swimming stage (see Scheltema, 1978, 1989; but see Johannesson, 1988; O'Foighil, 1989). Species without a free-swimming planktonic larval stage should also be geologically short-lived, and show higher speciation and extinction rates (Jablonski, 1986; but see Hedgecock [1986] for alternative interpretations of evolutionary significance of larval dispersal). According to certain paleontological studies, these predictions have been corroborated in late Cretaceous and Tertiary gastropods (Hansen, 1978, 1980; Jablonski, 1986, 1987). Bivalves apparently do not conform to such predictions, however (see Jablonski and Lutz, 1978; Stanley, 1986). In the present study, 5 out of the 10 most common benthic shelled-invertebrates found drifting in off-bottom collectors were bivalves, of which 3 were brooders. Possibly, the widespread occurrence of post-metamorphic drifting as a common feature in the life history of numerous bivalve species, including both species with and without planktonic larval stage, may have been one of the factors responsible for this apparent lack of correlation between the mode of larval development and the present and past geographical range of bivalves.

In conclusion, results of the present study, coupled with previous work, indicate that, regardless of whether the species has a planktonic larval stage, drifting of early life stages of gastropods and particularly bivalves, represents an important component of their early life-history. The prevalence of dispersal by juvenile drifting may imply the existence of ontogenetic shifts in microhabitat or habitat use as a common life-history trait in many small benthic molluscs. Thus, drifting could constitute an effective alternative means of transportation of otherwise sedentary or sessile organisms. In species that brood or produce benthic egg capsules with crawl-away juveniles, frequent drifting excursions could increase rafting opportunities and enhance long distance dispersal, thus favoring gene flow between populations. Juvenile drifting could have significant implications in biogeography and macroevolution in marine benthic invertebrates and may well be one of the factors responsible for the wide geographical distributions of many species with direct development.

2. Behaviour of Lacuna and properties of drifting mucous threads

The study of the behaviour of Lacuna spp. in the laboratory indicated that these snails can initiate drifting, particularly when exposed to oscillating water currents. The high numbers of juvenile Lacuna spp. found daily in collectors and numerous laboratory observations of the initiation of drifting strongly suggest that voluntary drifting is part of Lacuna's behavioural repertoire. Because of the importance of post-metamorphic drifting to the dispersal and recruitment of many small gastropods and bivalves, it is also likely that the juveniles of other species (e.g. mussels) display similar behaviours. The incidence of such behaviour is unknown in most species, however, and warrants more detailed investigation.

There have been no published reports on the length of the drifting mucous threads produced by gastropods. In the present study, Lacuna vincta were observed to produce mucous threads 50-150 times the length of the animal, with a 2 mm juvenile producing a thread 160 times its shell length. Lane et al. (1985) studied the drifting byssal threads of juveniles of the mussel Mytilus edulis (shell length of approx. 0.5-1.1 mm) and reported similar thread length / shell length ratios, although their values did not come from direct measurements but rather from calculations relating sinking rates and drag.

The production of a mucous thread in Lacuna spp. created a 4- to 8-fold reduction in sinking rates. Upward flows of only 0.4-1.0 cm / s are sufficient for juveniles $\leq$ 2 mm to remain suspended in the water column. These results also showed the superior ability of juveniles $\leq$ 2.5 mm to drift in the water column. On the other hand, even large juvenile and adult Lacuna spp. are capable of water column drifting if upward water velocities are on the order of 3-8 cm / s. In semi-exposed rocky intertidal areas such as at Prasiola Point, even during calm days, water currents created by ground swell and surge are much greater than a few centimeters per second. Such conditions, therefore, likely provide sufficient water velocities to keep both small and large Lacuna spp. in the water column.

Moreover, results obtained on sinking rates in Lacuna variegata revealed that, contrary to Johnson and Mann's conclusion (1986), extension of the foot and antennae did not

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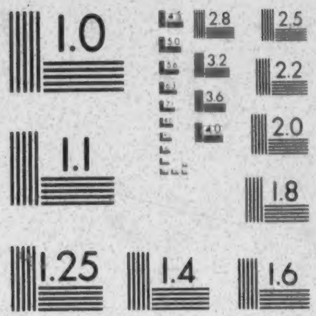
1.0
2.8
2.5
3.2
2.2
3.6
4.0
2.0
1.1
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MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

significantly reduce sinking rates. Only the production of a mucous thread effectively modifies the animal's sinking rate. This was also found to be true for *Nucella emarginata*.

Laboratory experiments in which juvenile snails were spun in a finger bowl suggest that *Lacuna* spp. and *Barleeia* spp. secrete enough mucus to generate a long thread. This was not the case with juvenile *Littorina sitkana* or *Nucella emarginata*. Significant reductions in sinking rates of newly-hatched individuals of these two species, however, suggested that when the snails were dislodged, the mucus already produced by the foot in contact the substratum can be stretched to generate a functional mucous thread as the animal leaves the substratum. Thus, although newly-hatched juvenile *L. sitkana* and *N. emarginata* do not appear to be as specialized as *Lacuna* spp. or *Barleeia* spp. for drifting (see data on collectors), mucus trailing behind the animal can significantly increase time spent in the water column. Because of the presence of mucus and mucous glands in the foot of gastropods, mucus trailing behind dislodged newly-emerged or newly-metamorphosed juveniles may be prevalent in gastropod species other than those mentioned. Such mucous threads can also greatly enhance the ability of snails to get hold of a substratum while drifting.

The attachment of larvae and post-larval stages by byssal threads has been reported in the mussel *Mytilus edulis* (de Block and Tan-Maas, 1977; Eyster and Pechenik, 1987). As demonstrated in this study, an important function of gastropod mucous threads is enhancing the animal's ability to attach to a substratum (e.g. algae) while drifting in the water column. Vahl (1983) had proposed a similar function for the mucus in the limpet *Helcion pellucida* living on the kelp *Laminaria*. In semi-exposed intertidal seaweed communities, where water turbulence is not a limiting factor for maintaining snails in suspension, the ability of the mucous thread to enable drifting snails to attach themselves effectively to algae, may well be one of its most important functions.

3. Life history and types of mucous threads

The functions of mucus in molluscs are multiple, and include dispersal (drifting) and attachment (see review by Prezant [1985] on molluscan mucins). The present study shows that there are distinct differences in the structure of mucous threads produced by drifters (e.g. *Lacuna* spp. and *Barleeia* spp.) and attachment threads produced by non-drifters. The neogastropod *Alia gouldi*, which does not drift, uses its thread as an anchor line. Although the diameter of the threads of drifters and non-drifters are similar, they differ in the organization or orientation of their fibers. Drifting threads have high numbers of parallel fibers, but the attachment thread of *A. gouldi* is made up of at least two types of helically coiled fibers.

In an ultrastructure investigation, Lane *et al.* (1985) studied both the drifting and attachment threads of newly-metamorphosed juvenile Mytilus edulis (shell length < 1 mm). They reported that although the two types of threads were about the same diameter (1-3 µm), they differed in structural complexity. They found that the drifting thread was made of only one filament and showed no evidence of internal sub-substructure. In contrast, attachment threads had a more complex structure and were composed of many filaments. This difference in structure and complexity between the two types of threads produced by mussels thus compares with my observations on drifting and non-drifting (attachment) threads in several species of gastropods. The configuration of Lacuna's and Barleeia's mucous thread, with its numerous parallel fibers, may enable stretching, which in turn greatly enhances the hydrodynamic drag on the snails. The numerous parallel mucous fibers could originate from the secretion of individual mucous glands distributed throughout the epithelium of the foot sole. The synthesis of these mucous fibers was not investigated in the present study.

Contrasting with drifting mucous threads, the two different coiled components of Alia gouldi's thread are likely responsible for its strength ana suggests fundamental differences in mechanical properties, such as elasticity and strength, between drifting and non-drifting attachment threads.

In addition, observations under a dissecting microscope of Alia gouldi's mucous threads bundled up behind the animal's foot as it was suddenly detached revealed that the mucous produced was whitish in color, compared with transparent threads produced by drifters like *Lacuna* spp. (Martel, unpublished observation). The colour difference suggests differences in the biochemical composition of the threads between these gastropods. There may be a high proteinaceous component in *Alia*'s mucous thread (collagen or other related proteins) which could give strength to the thread. High protein (including collagen) content is responsable for the strength of attachement byssal threads in bivalves (see review by Waite, 1983).

The use of attachment devices (byssal threads) is most widespread and developed in bivalve molluscs (see Waite, 1983; Yankson, 1986). The occurrence of temporary attachment threads, however, has also been reported in several gastropods living in algal habitats (Mooers, 1981; Auster, 1982; Houbrick, 1987). The best known example is that of the brown sargassum snail *Litiopa melanostoma*. This gastropod lives among offshore floating mats of *Sargassum*, and, according to Houbrick (1987) has a "metapodial mucous gland that produces a strong mucous thread, anchoring the snail to its algal habitat". In that habitat, the attachment mucous thread not only allows the snail to move effectively between the many branches of this complexly structured habitat, but also prevents it from falling off the alga and sinking into the deep sea. There has been, to my knowledge, no study of the structure of *L. melanostoma*'s mucous thread, therefore preventing a comparison with that of *Alia gouldi*.

Details of the synthesis of the mucous thread of *Lacuna* spp. and *Alia gouldi*, including the different tissues, organs and biomechanics involved, await further investigation. Comparisons of the structure, biomechanical properties and biochemical composition of the various types mucous threads used by gastropods, including those reported in the present study, would certainly yield highly valuable information on the role of mucus in the life history of marine gastropods.

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Chapter IV.

The effects of post-metamorphic dispersal (drifting) and substrate selection on recruitment patterns and life-history parameters in intertidal Lacuna spp.

A. INTRODUCTION

Recruitment and population biology of herbivorous gastropods living on rocky substrata in the intertidal zone have been the object of many studies (littorines: Emson and Faller-Fritsch, 1976; Raffaelli and Hughes, 1978; Hughes, 1980; Hughes and Roberts, 1981; McCormack, 1982; limpets: Sutherland, 1970; Underwood, 1975 a, b; Creese, 1980; trochids: Jardine, 1986) as well as on gastropods living on intertidal macroalgae (Barleeia: Southgate, 1982 b; Patina; Graham and Fretter, 1947; Vahl, 1971; Rissoa: Wigham, 1975; Borja, 1986; Tricolia: Fretter and Manly, 1977) (see review by Underwood, 1979).

Among the most abundant gastropods living and feeding on seaweeds are the prosobranchs of the genus Lacuna, which are distributed in many oceans of the world, including the North Pacific, North Atlantic and Arctic Oceans (Abbott, 1974). During the past two decades several studies of Lacuna have dealt with various aspects of population biology in subtidal (Smith et al., 1985; Johnson and Mann, 1986) and intertidal habitats (Smith, 1973; Fretter and Manly, 1977; Ockelmann and Nielsen, 1981; Southgate, 1982 a; Langan, 1984; Grahame, 1986). Studies on L. vincta along British coasts have shown that this species completes its life span within one year and have revealed that populations fluctuate widely during the year and are characterized by sharp decreases in density of small juveniles in the weeks or months following larval settlement (Smith, 1973; Fretter and Manly, 1977; Southgate, 1982 a; Grahame, 1986). It has been postulated that such decreases in juvenile density of *L. vincta* are due to high mortality (unknown causes) occurring after settlement.

An important feature of the dynamics of populations of *Lacuna vincta* in rocky intertidal seaweed communities has been reported by Grahame (1986) and Southgate (1982 a). They observed increases in density of large individuals on certain species of seaweeds in late fall, prior to the spawning season, but long after the spring/summer recruitment periods. Similarly, Langan (1984) reported sudden increases in density of adults (shell length > 2 mm) of both *L. marmorata* and *L. unifasciata* on the intertidal surfgrass *Phyllospadix torreyi* in California. These authors suggested that such sudden increases in density were caused by immigration of snails to the habitat.

Recent studies have demonstrated the drifting and dispersal capabilities of several gastropod species living on seaweeds. These include the limpet *Helcion pellucida* (Vahl, 1983) as well as at least two species of *Lacuna* from both subtidal (Johnson and Mann, 1986; Martel, 1987; Chapter II) and intertidal habitats (Martel, 1988; Chapter III). I demonstrated in Chapter III that *Lacuna* spp. produce mucous threads up to 160 times the length of their shell. Once the animal is in the water column, the mucous thread greatly increases the hydrodynamic drag and keeps the animal practically neutrally buoyant (Johnson and Mann, 1986; Martel, 1988). It also increases the drifting snail's chances of attaching to a new substratum (Chapter III). In addition, numerous post-metamorphic Lacuna spp. have been caught in all off-bottom collectors installed at Prasiola Point during spring, summer and fall of 1988 (Martel, 1988; see Chapter III).

The first part of the present study examines the recruitments and patterns of seasonal abundances of Lacuna vincta and L. variegata in a semi-exposed intertidal rocky area with references to the results on drifting and dispersal in Lacuna spp.. As many as four Lacuna habitats (seaweeds) differing both in structure and persistence (i.e. longevity or lifespan of the plant) have been monitored simultaneously in order to gain an overview of this highly dynamic system. The first part of this study has two specific objectives. Objective #1 is to describe the seasonal patterns of abundances and size-frequency distributions of Lacuna vincta and L. variegata on four types of seaweed. This includes examining the role of post-metamorphic drifting as a mechanism which would explain varying abundances of snails at certain times of the year. Objective #2 is to examine the presence of shelters, such as pits and bullae (depressions on the surface of kelp blades) and their role as a determinant in the abundance of intertidal juvenile *Lacuna* spp.. Seasonal variations in the abundance of juvenile snails are compared with seasonal changes in blade morphology occurring in the kelp *Hedophyllum sessile*.

The effects of food quantity as well as quality on the somatic and gonadal growth have been investigated in few benthic marine invertebrates (polychaetes: e.g., Gremare, 1988; Qian, 1989 a, b; bivalves: Epifanio, 1979; MacDonald and Thompson, 1985 a, b; Barber *et al*., 1988; Grant and Cranford, 1989). Little is known, however, of the effects of substratum choice (algae) on growth of newly-metamorphosed juveniles to the adult stage, on maximal adult size, on reproductive output and on lifetime fecundity. To my knowledge, such a study has not been conducted on a marine gastropod. Part of the difficulty lies in finding a system for which such life-history parameters can be tested within a relatively short time-span. *Lacuna* spp. are easy to raise, breed in tanks, grow quickly (Grahame, 1977, 1982; Langan, 1984) and reproduce within 3-4 months of metamorphosis. Thus, *Lacuna* spp. represent a suitable system for such a study.

Lacuna occur on a variety of algae (Bishop and Bishop, 1973; Smith, 1973; Ockelmann and Nielsen, 1981; Southgate, 1982 a; Langan, 1984). Fretter and Manly (1977) reported that dense tufts of red algae are important settlement sites for the larvae of *L. vincta* and that adult *L. vincta* are found on various seaweeds. Southgate (1982 a) proposed that red turf algae are a nursery habitat for early life stages of L. pallidula and reported a shift in habitat which may reflect changes in dietary preference as juveniles grow.

The second part of this study examines the consequences of Lacuna's relocation to various algal substrata. For organisms like Lacuna spp. whose substratum is also their food, the choice of a particular habitat or alga could have significant implications on life-history parameters such as growth and fecundity. Thus, the objective of this second part is to show how habitat choices made by drifting juvenile and adult Lacuna spp. influence certain life-history parameters (growth, age and size at sexual maturity, sexual dimorphism and reproductive output).

B. MATERIALS AND METHODS

1. Study sites and seaweed communities

To monitor abundance and size-frequency distributions of Lacuna vincta and L. variegata, various species of seaweeds were sampled monthly in two semi-exposed low intertidal rocky habitats. Abundance of seaweeds at the sites was also monitored. At Prasiola Point (Fig. 2.1, see Chapter II), three types of intertidal seaweeds were sampled: (1) Hedophyllum sessile, (2) Halosaccion glandiforme and (3) the red turf algae (Odonthalia floccosa, Polysiphonia sp., Cryptosyphonia sp., Laurencia sp., and Prionitis sp.). H. sessile and, to a lesser extent, H. glandiforme, cover large patches of bedrock in the mid-intertidal zone. Red turf algae, however, form more heterogenous communities, with many species similar in structural complexity -- highly ramified, bushy algae -- occurring within a small area. At Execution Rock (Fig. 2.1, see Chapter II) Iridaea cordata dominates a boulder-covered low intertidal area.

As habitats for Lacuna spp., the above-mentioned algae differ markedly in their life cycles and persistence. Halosaccion glandiforme and many red turf algae are annual, (thus disappearing completely) or perennial (only a small meristematic portion of the plant overwinters attached to the bedrock). In contrast, like many laminarians, a high percentage of Hedophyllum sessile overwinters. According to Widdowson (1965), H. sessile can live more than two years. At Prasiola Point, H. sessile thus represents one of the persistent habitats where Lacuna spp., particularly L. vincta, can overwinter and complete its life cycle.

2. Methods of sampling: seaweeds

A quadrat of 0.1 m^2 (0.317 X 0.317 m) was randomly thrown among patches of the intertidal seaweed communities to sample marine macrophytes. Because of the heterogeneity and the patchiness of the sampled algae, the 0.1 m^2 quadrat had to be thrown while looking at the substratum. For each quadrat the seaweeds were cut as close to the bedrock as possible and put into plastic bags. Wet weight of the seaweeds was determined in the laboratory (nearest 0.1 g).

3. Methods of sampling: Lacuna spp.

Lacuna spp. were taken from the above-mentioned seaweed quadrats. The small size and cryptic colour of the snails made it impossible to assess the abundance of these Lacuna spp. while looking at the area where the quadrat was thrown. Only close visual inspection of the plants permitted an assessment of snail abundance. In addition, there was no evidence of any relationship between the biomass of algae found within the quadrats (0.1 m^2) and the number of snails (Martel, pers. observation; Langan, 1984). These observations therefore support the randomness of the method employed to sample Lacuna. In the laboratory, snails were separated from the seaweeds by washing the algae in warm freshwater and were collected using Nitex filters. Shell length was determined under a dissecting microscope.

4. Seasonal changes in blade morphology in Hedophyllum sessile

Seasonal changes in blade morphology in the kelp Hedophyllum sessile were monitored by randomly sampling blades at the intertidal study site at Prasiola Point. Blades were examined for the presence of bullae -- numerous pits or depressions found at the surface of the plant (see Results, Figs. 4.3 and 4.4) -- and were categorized as: a) blade completely covered with bullae, b) blade (the meristem region) half covered with bullae and c) flat blade (without bullae).

Transverse sections, 1.5-2.0 mm thick, were taken using a scalpel guided by a ruler, 10-20 cm from the holdfast of *Hedophyllum sessile* blades randomly sampled in the field. Prints were taken of these thin sections placed sideways on the photographic glass surface of a Canon photocopier.

5. Importance of drifting in intertidal *Lacuna* spp. populations

The analysis of abundance and size-frequency distributions of individuals caught in off-bottom *Gracilaria pacifica* collectors (Fig. 3.1, see Chapter III) during spring, summer and fall, permitted the determination of the role of post-metamorphic drifting in intertidal *Lacuna* spp. populations. Details of the procedures for construction and installation of intertidal collectors, as well as extraction of snails, have been described in Chapter III.

To compare the efficiency of seaweeds varying in structural complexity to attract drifting *Lacuna* spp. a second type of collector was made by replacing *Gracilaria pacifica* with flat *Hedophyllum sessile* blades. Collectors were installed for 24 hours, after which time they were retrieved, washed on site in fresh water to extract and recover *Lacuna* spp. and then put back in the field.

6. Effect of diet on growth and fecundity in *Lacuna variegata*

The growth (mm / month) and fecundity (number of egg masses / female / unit time) of *Lacuna variegata* were compared between groups of snails feeding on one of three species of seaweeds on which it commonly occurs: *Iridaea cordata*, *Ulva lactuca* and *Odonthalia floccosa*. *L. variegata* used for this experiment were < 1 mm and originated from the turf algal communities at Prasiola Point. The size of each disc-shaped *L. variegata* egg masses was determined by measuring its surface.

7. Field evidence of habitat-related differences in adult size, sexual dimorphism and size of egg masses in *Lacuna vincta*

Lacuna vincta were sampled in the field in order to study habitat-related differences in sexual dimorphism, size-frequency distributions of adult males and females as well as size of egg masses deposited. The animals were sampled from Prasiola Point (*Hedophyllum sessile*) and Grappler Inlet (*Fucus disticus* and *Zostera marina*) (Fig. 2.1, see Chapter II). Samples were taken during the winter breeding period (January-March) 1988. The animal was put foot upward in a shallow finger bowl filled with seawater and its sex determined by looking for the presence of a penis as the animal extended and twisted its foot. Egg masses were removed from algal blades with a thin metal blade, dried at

60° C for 24 hours, and the dry weight determined to the nearest 10 μg.

8. Long-term effects of substratum choice on growth rates, size and lifetime fecundity in Lacuna vincta:

Series I (newly-metamorphosed juveniles to adults)

Growth and fecundity experiments were conducted by raising newly-metamorphosed juvenile Lacuna vincta (< 1 mm) in plastic 5 cm Petri dishes with 600 μm Nitex windows. Juveniles were fed one of the following seaweeds: Nereocystis luetkeana, Macrocystis integrifolia, Ulva lactuca, or a mixture of branched red turf algae (Polysiphonia sp., Prionitis lyalli and Laurencia spectabilis). L. vincta used for these experiments were from Macrocystis beds in the vicinity of Grappler Inlet and Dixon Island (Fig. 2.1, see Chapter II). Animals were randomly assigned to a Petri dish (5-10 snails / dish) and food was added weekly. Measurements of shell length and deposition of egg masses were recorded every 2-4 weeks. The sea-water temperature for the duration of the experiment (180-210 days) was 9-11° C. The total number of eggs per egg mass was determined using a regression equation of dry weight / number of eggs.

9. Long-term effects of substratum choice on growth rates, size and lifetime fecundity in *Lacuna vincta*: Series II (large juveniles to adults)

Growth and fecundity of juvenile *Lacuna vincta* (two size-groups: 2.6-2.8 mm and 3.15-3.20 mm shell length) feeding on semi-exposed intertidal seaweeds on which they naturally occur (*Hedophyllum sessile*, *Fucus disticus*, *Iridaea cordata* and *Odonthalia floccosa*) were studied in the laboratory. Growth rates and fecundity on *Macrocystis integrifolia* were studied for comparison purposes. Snails for this experiment originated from *Laminaria saccharina* plants growing at the kelp farm (Fig. 2.1, site "k", see Chapter II).

10. Short-term effects of diet shifts on size and fecundity of sexually mature *Lacuna vincta*

Experiments on the short-term effects of changes in algal diet were conducted to test the effect of moving from one intertidal seaweed to another on the growth and reproductive output of sexually mature female *Lacuna vincta*. Snails from the kelp farm feeding on *Laminaria saccharina* were used. Male and female *L. vincta* selected for this experiment had ripe gonads (the translucent shell allows inspection of the state of the gonad by observing the first few coils of the animal under a dissecting microscope). For 36 days, mature females (average: 5.61 mm shell length, SD = 0.359 mm, n = 43) and mature males were placed in Petri dishes (10 cm) with nitex windows containing one of either Hedophyllum sessile, Iridaea cordata, Fucus disticus or Odonthalia floccosa (hereinafter referred to by genus only). Three or 4 females and 2 or 3 males were put in each of 20-22 petri dishes per species of seaweed tested. Egg masses deposited were removed every 6 days.

After 18 days, snails of 10 or 11 of the original 20-22 petri dishes for each diet were transferred to a different seaweed as follows: Hedophyllum to Odonthalia, Odonthalia to Hedophyllum, Iridaea to Hedophyllum and Fucus to Hedophyllum. Snails from the other 10 to 11 petri dishes were maintained on their original diet throughout the experiment. The shell length of females was measured after 12, 30 and 36 days.

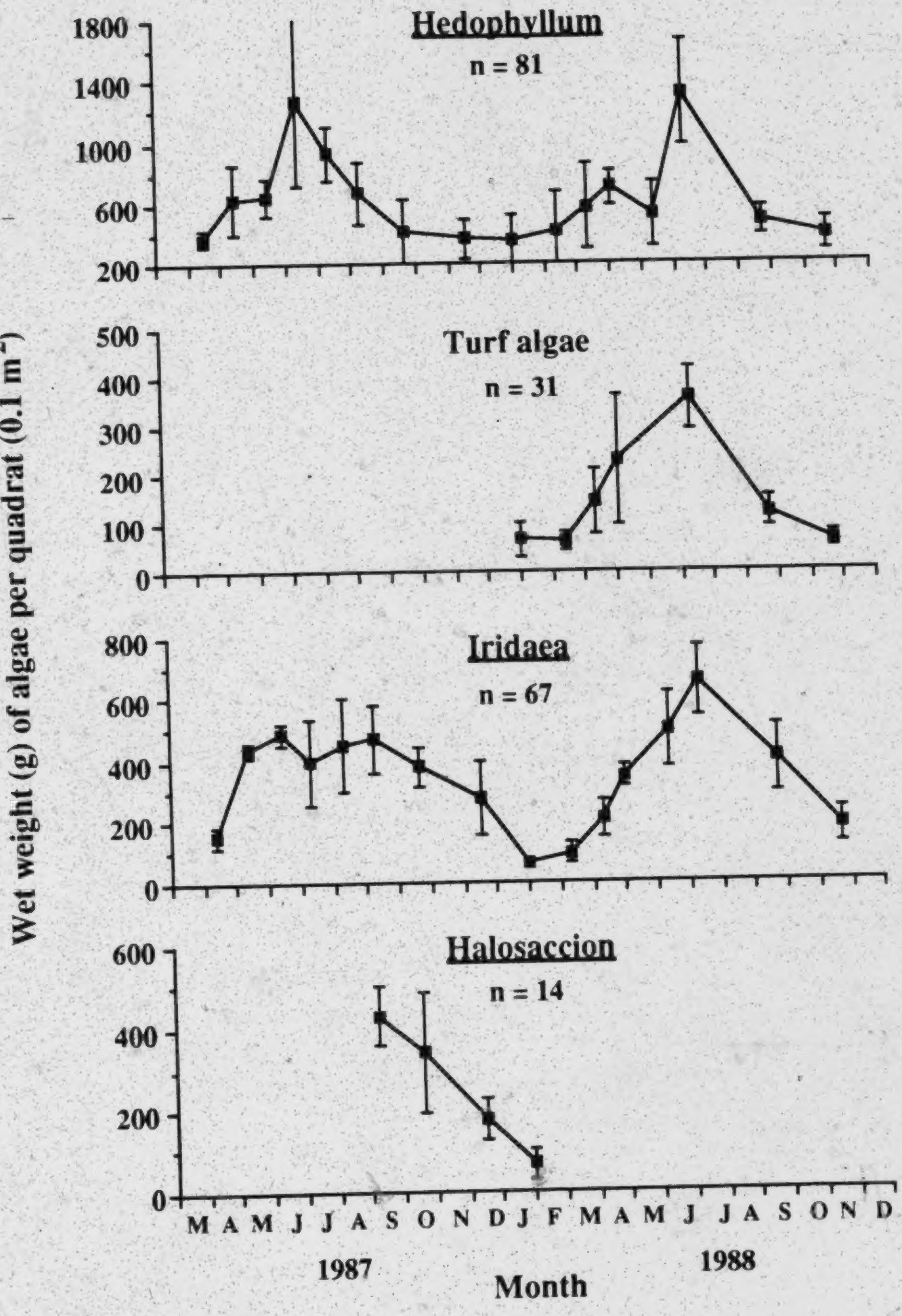
Statistical analyses follow procedures described in Sokal and Rohlf (1981).

C. RESULTS

1. Seasonal abundance of seaweeds

The biomass of all seaweeds sampled at Prasiola Point and Execution Rock followed an annual seasonal cycle of abundance (Fig. 4.1). For both 1987 and 1988 biomass of seaweeds significantly increased from winter to summer with highest biomass during late spring/summer, while the trend reversed from summer to winter (Kruskal-Wallis ANOVA, $p < 0.05$) (Fig. 4.1). Reduced photoperiod and heavy storms led to sparse seaweed populations during the winter. Thus, there is a strong seasonal component to the Lacuna spp. habitat.

Figure 4.1. Seasonal variations in biomass of four intertidal algae at Prasiola Point during 1987 and 1988. Points show mean wet weight (g) of algae per 0.1 m^2 quadrat (0.317 m X 0.317 m). The n value represents the total number of quadrats (3-7 per monthly sample). Error bars represent ± SD.


Hedophyllum
n = 81
1800
1400
1000
600
200
Turf algae
n = 31
500
400
300
200
100
0
Iridaea
n = 67
800
600
400
200
0
Halosaccion
n = 14
600
400
200
0
Wet weight (g) of algae per quadrat (0.1 m^2)
M A M J J A S O N D J F M A M J J A S O N D
1987
1988
Month

Compared to other seaweeds, the biomass of the long-lived *Hedophyllum sessile* remains comparatively high (about 400 g / 0.1 m^2) during the winter (Fig. 4.1).

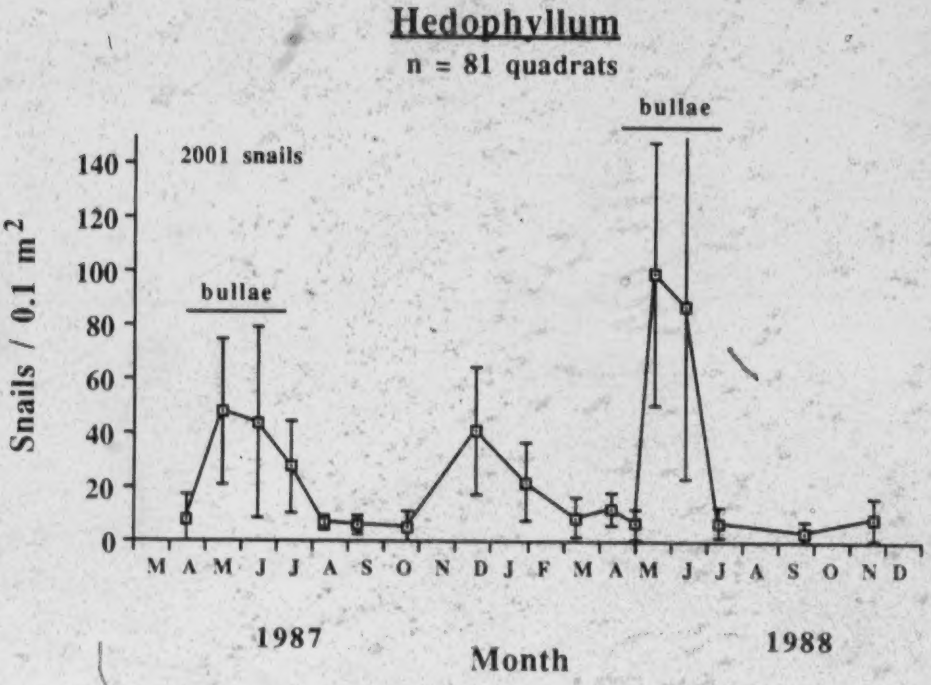
2. Population dynamics of *Lacuna* spp. on *Hedophyllum*: importance of plant morphology and post-metamorphic drifting

a. Importance of plant morphology in abundance of *Lacuna* spp.

Abundance of *Lacuna* spp. on *Hedophyllum* at the study site at Prasiola Point showed two periods of high density during the year: one during the late spring/early summer (April-July 1987: Kruskal-Wallis ANOVA, $H = 3.857$, $p < 0,05$; April-June 1988: $H = 17.8$, $p < 0,005$) and the other during late fall/early winter (September-January 1988, $H = 10.16$, $p < 0.02$) (Fig. 4.2). During the late spring/early summer average densities were between 44 and 100 individuals per 0.1 m^2 quadrat. For both 1987 and 1988, there was a time lag of 2-4 weeks between the timing of peak larval settlement, which occurred during April/early May (see Figs. 2.5, 2.6, Chapter II), and the arrival of recruits in the *Hedophyllum* habitat (Fig. 4.2).

A survey of *Hedophyllum* at Prasiola Point revealed that the rapid increase in density during May/June coincided with the presence of young *Hedophyllum* blades. Contrasting with the smooth, flat blades found during the fall and winter, these young *Hedophyllum* blades growing during the spring are

Figure 4.2. Seasonal abundance of *Lacuna* spp. on the kelp *Hedophyllum sessile* at Prasiola Point during 1987 and 1988. Points show mean number of snails per 0.1 m^2 quadrat (0.317 m X 0.317 m). The n value represents the total number of quadrats (3-7 per monthly sample). The two horizontal bars indicate approximately when *Hedophyllum* blades were bullated (late spring/summer). Error bars represent ± SD.

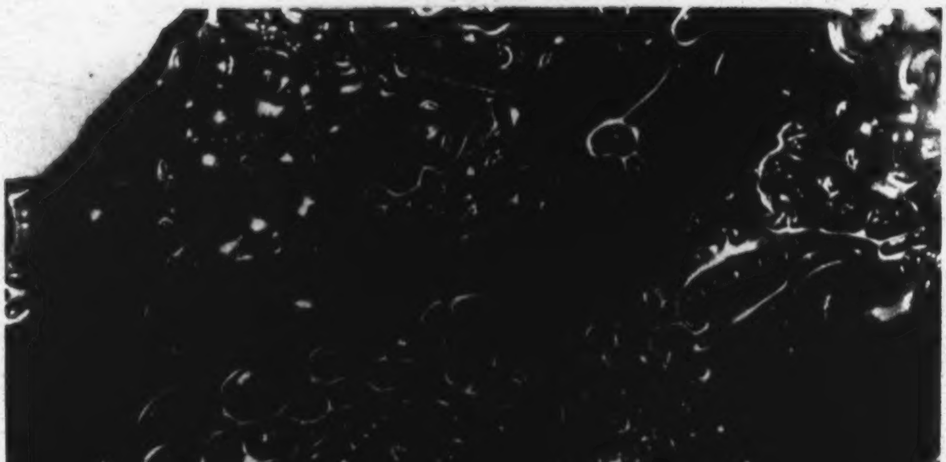

Hedophyllum
n = 81 quadrats
2001 snails
bullae
bullae
Snails / 0.1 m^2
0
20
40
60
80
100
120
140
M A M J J A S O N D J F M A M J J A S O N D
1987
1988
Month

pitted or bullated (Figs. 4.2, 4.3, 4.4). During the spring, snails living on *Hedophyllum* were almost exclusively found in the bullae. The meristem of these growing young blades became gradually flat and pushed the older bullated tissues toward the distal end (Figs. 4.4, 4.5 A). The proportion of bullated to flat blades changed markedly during that period (G-test, G(Williams) = 96.02, $p < 0.001$) (Fig. 4.5 A) and was correlated with a decrease in *Lacuna* spp. density (Kruskal-Wallis ANOVA, $H = 9.27$, $p < 0.01$) (Fig. 4.5 B). During late summer/early fall *Hedophyllum* blades at Prasiola Point were smooth and flat, and the density of snails on these blades was at its lowest (Figs. 4.4, 4.5; also see Fig. 4.2).

The importance of bullae among which *Lacuna* spp. find shelter while living on *Hedophyllum* was indicated in the samples taken during late July 1989, when both flat and bullated blades occurred (Fig. 4.6 A). The average density of *Lacuna* spp. on *Hedophyllum* blades with bullae was 4.56 / blade, compared to only 0.17 / blade on flat blades, a 26-fold factor (Mann-Whitney 2 Sample Test, $Z = 8.233$, $p < 0.001$) (Fig. 4.6 A). In addition, within-blade distributions of *Lacuna* spp. on 47 randomly selected *Hedophyllum* blades showed a similar pattern, with 187 snails in the distal half covered with bullae compared to only 24 individuals in the proximal flat half (region with bullae: mean = 3.979 snails, SD = 4.799; flat region, mean = 0.511, SD = 0.906) (G-test, G(Yates) = 76.342, $p < 0.001$) (Fig. 4.6 B).

Figure 4.3. Photographs showing flat and bullated Hedophyllum sessile blades sampled at Prasiola Point. A) Flat blades (mainly found during the fall and the winter) (top of picture) and young bullated blades (found in late spring/summer) (bottom of picture). Also note the difference in blade width between the two morphs. Ruler (15 cm) indicates scale in the center of the picture. B) Close up picture showing the details of the pits and bullae found at the surface of bullated blades (summer 1989).

A



B

Figure 4.4. A, B. Thin sections of Hedophyllum sessile blades sampled during the winter and early spring at Prasiola Point. Pictures represent photocopies of thin cross-sections of blades taken 10-20 cm from the holdfast. A) Fall/winter: flat blades (sampled on December 23, 1988). B) Late spring: young bullated blades (sampled on May 04, 1989). Magnification: 0.5 X.

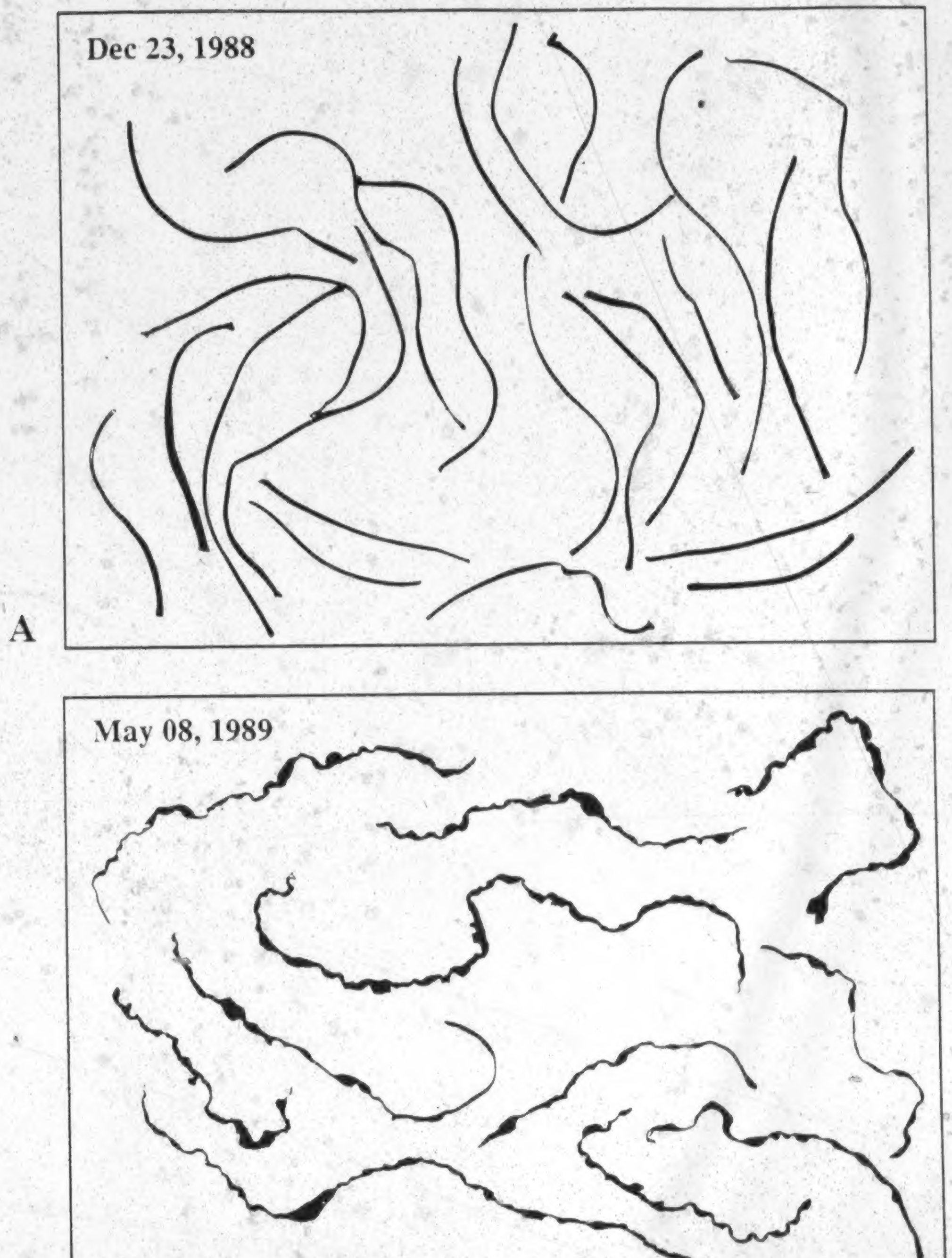
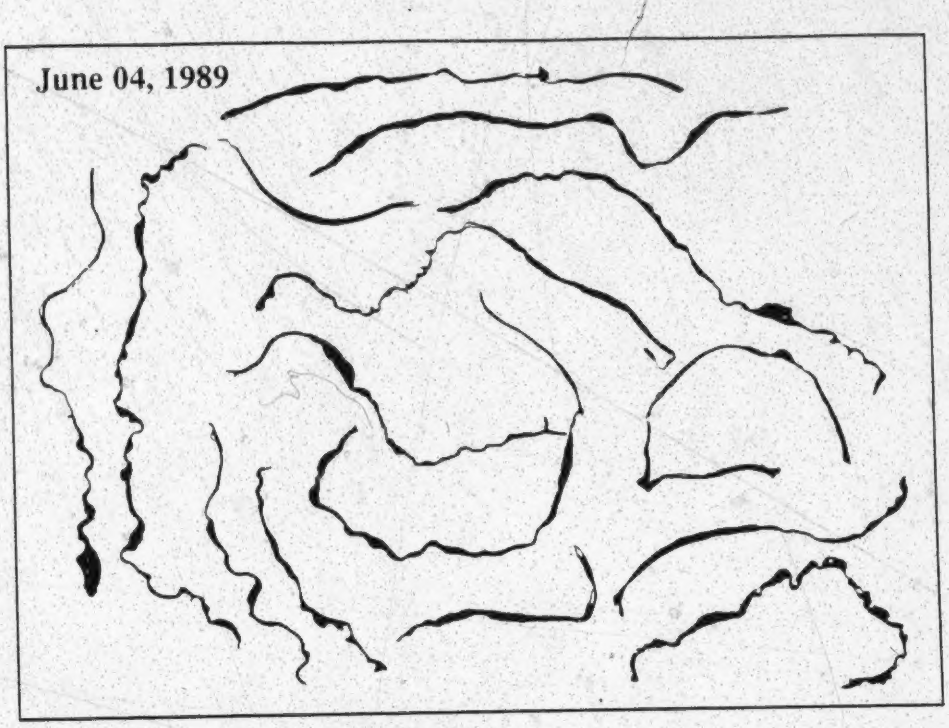
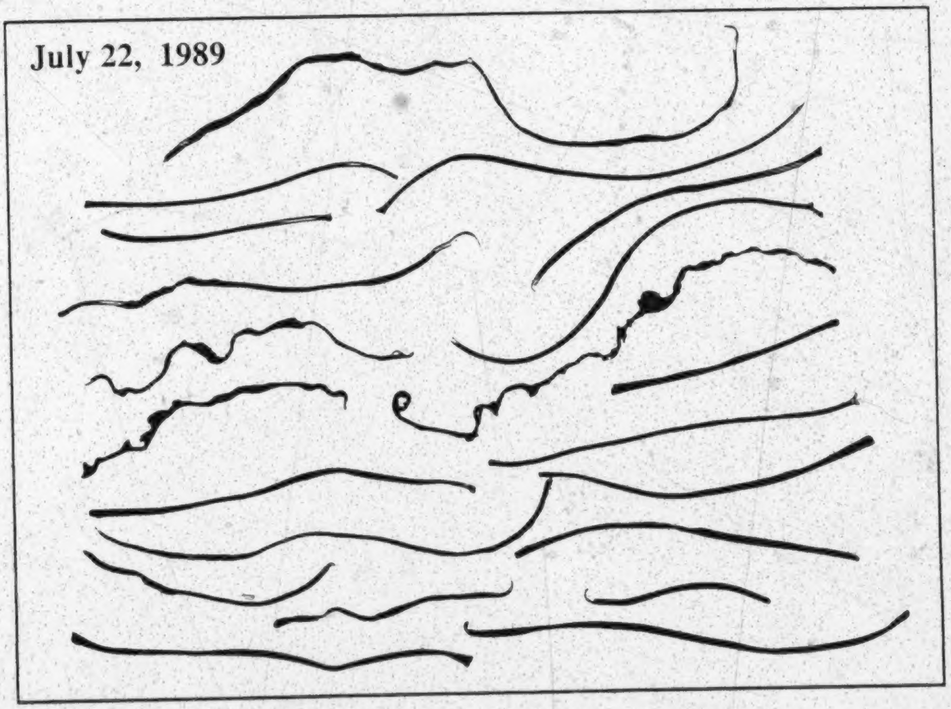

Dec 23, 1988
A
May 08, 1989
B

Figure 4.4. C, D. Thin sections of Hedophyllum sessile blades sampled during late spring and summer at Prasiola Point. Pictures represent photocopies of thin cross-sections of blades taken 10-20 cm from the holdfast. C) Late spring: bullated blades. Note beginning of occurrence of flat blades (sampled on June 06, 1989). D) Mid-summer: transition, bullated blades and increasing numbers of flat blades (sampled on July 22, 1989). Magnification: 0.5 X.


June 04, 1989

C


July 22, 1989

D

Figure 4.5. Morphology of Hedophyllum sessile blades and density of Lacuna spp.. A) Changes in blade morphology of H. sessile at Prasiola Point during the late spring/summer. Histograms show proportion of bullated blades, half bullated / half flat blades, and entirely flat blades in quadrat samples. Numbers below each date indicate number of H. sessile blades sampled. B) Density (snails/0.1 m^2) of Lacuna spp. per 0.1 m^2 quadrat (0.317 m X 0.317 m) of H. sessile habitat at Prasiola Point during the same period. Error bars represent ± SD.

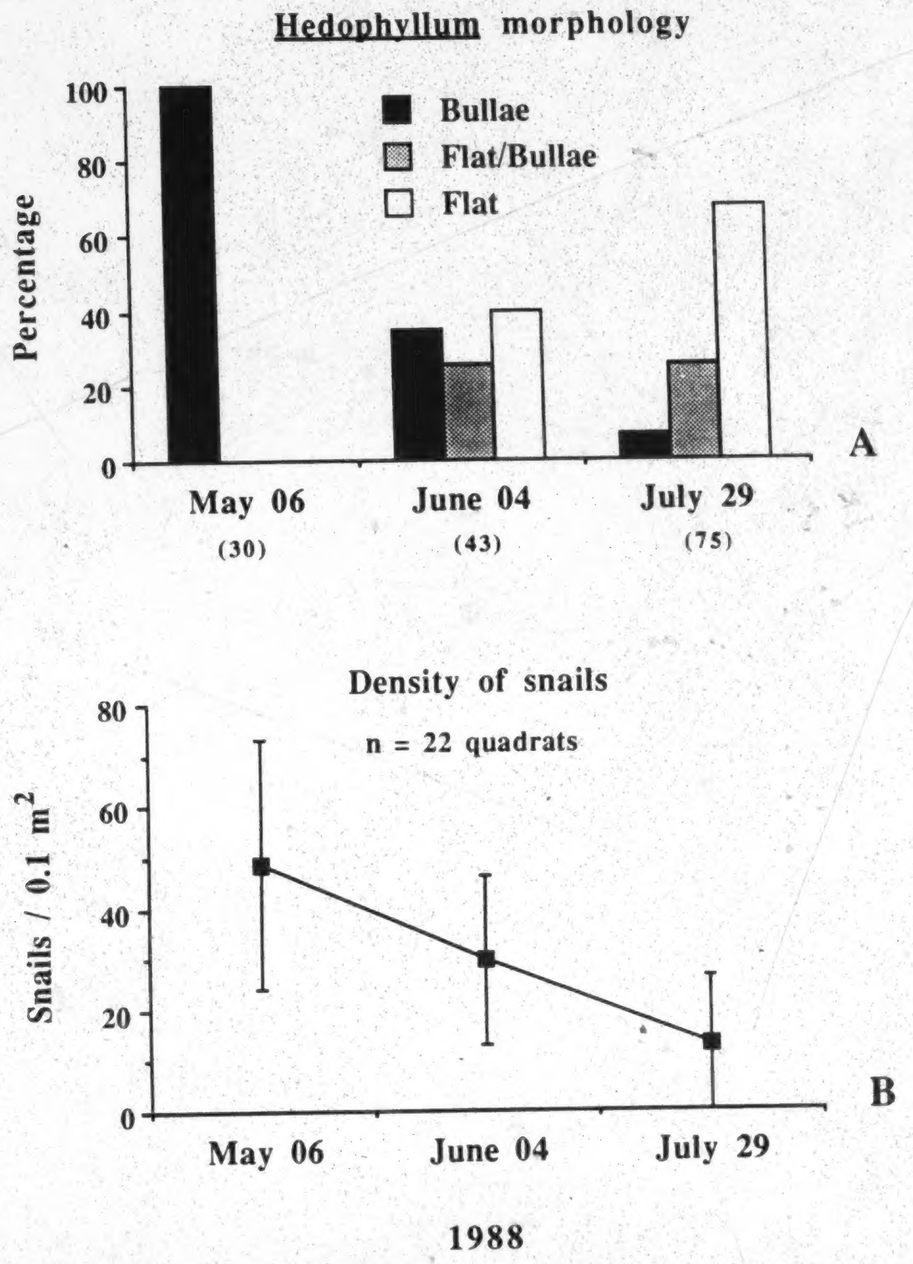
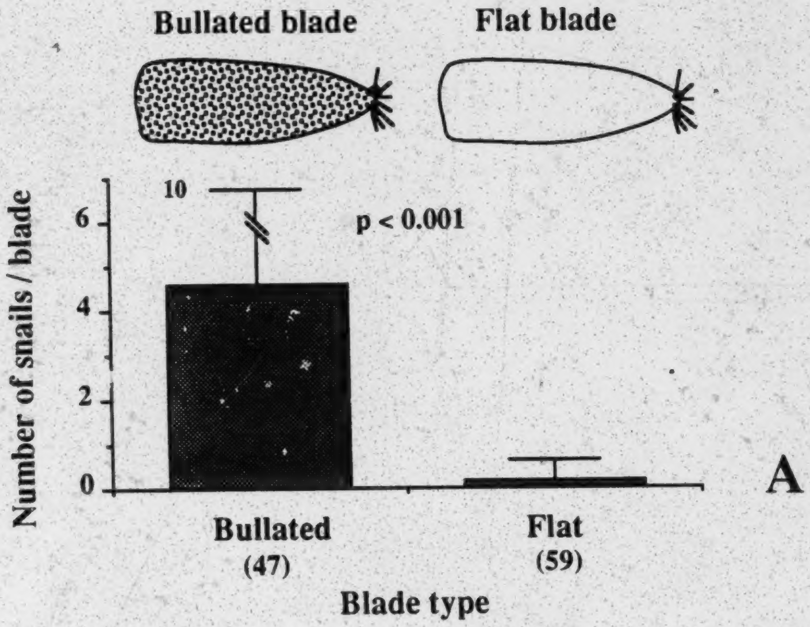
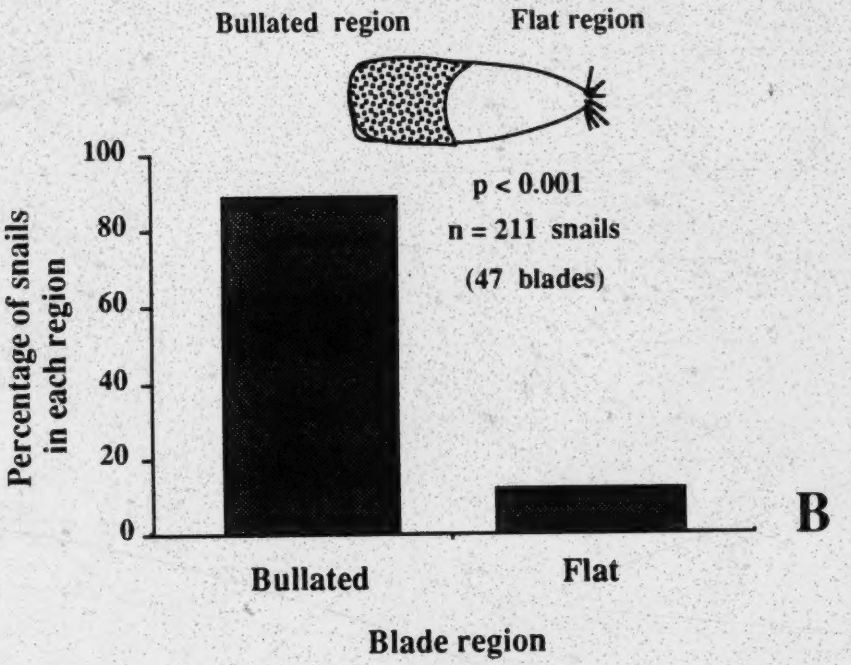

Hedophyllum morphology
100
80
60
40
20
0
Percentage
■ Bullae
▨ Flat/Bullae
☐ Flat
A
May 06
(30)
June 04
(43)
July 29
(75)
Density of snails
n = 22 quadrats
80
60
40
20
0
Snails / 0.1 m²
B
May 06
June 04
July 29
1988

Figure 4.6. Comparison of abundances of Lacuna spp. on bullated and flat tissues of Hedophyllum sessile from samples taken at Prasiola Point during late July 1989. A) Comparison between bullated blades and flat blades. Numbers below blade-type indicate number of blades sampled. B) Comparison between the bullated and the flat regions in blades half bullated/half flat.


Bullated blade
Flat blade
Number of snails / blade
10
6
4
2
0
p < 0.001
Bullated
(47)
Flat
(59)
Blade type
A


Bullated region
Flat region
Percentage of snails in each region
100
80
60
40
20
0
p < 0.001
n = 211 snails
(47 blades)
Bullated
Flat
Blade region
B

At Prasiola Point, bullae-covered Hedophyllum was absent during the winter (Figs. 4.2, 4.3, 4.4). At that time, snails were usually found inside folds or between blades, close to the holdfast of the plant.

b. Immigration and importance of juvenile drifting

Size-frequency distributions of Lacuna spp. on Hedophyllum for both 1987 and 1988 revealed that the sharp spring increases in snail density following the appearance of young blades covered with bullae were caused by the sudden arrival of juveniles in the habitat (modes at 1.50-1.75 mm) (Fig. 4.7 A, B). Juveniles arrived several weeks after the peak period of larval settlement (April/early May; see Chapter II). During spring recruitment periods on Hedophyllum, Lacuna spp. of $\leq$ 1 mm shell length represented only a very small proportion of the total number of newly-arrived snails (Fig. 4.7 A, B). Thus, settlement of Lacuna spp. larvae on Hedophyllum was very low and recruitment was realized by juveniles arriving in the habitat.

Between 34.4 and 42.8% of all Lacuna spp. caught in off-bottom intertidal Gracilaria collectors during early May 1988 (spring recruitment period) were > 1 mm shell length (Fig. 4.8). Such high proportions of drifting juvenile > 1 mm greatly influence patterns of recruitment and population dynamics of intertidal Lacuna spp.. In addition, because larval settlement occurs at 700-850 µm shell length (Fig. 2.7, Chapter II) the 1 mm size-limit for separating individuals arriving as larvae from those arriving as

Figure 4.7. A. Size distributions of *Lacuna vincta*, *L. variegata* and *L.* spp. on *Hedophyllum sessile* at Prasiola Point from April 15, 1987 through April 13, 1988. Histograms show average number of individuals of each size-class per 0.1 m^2 quadrat (0.317 X 0.317 m). Numbers below dates indicate total number of snails in samples (cont'd).

Lacuna on Hedophyllum

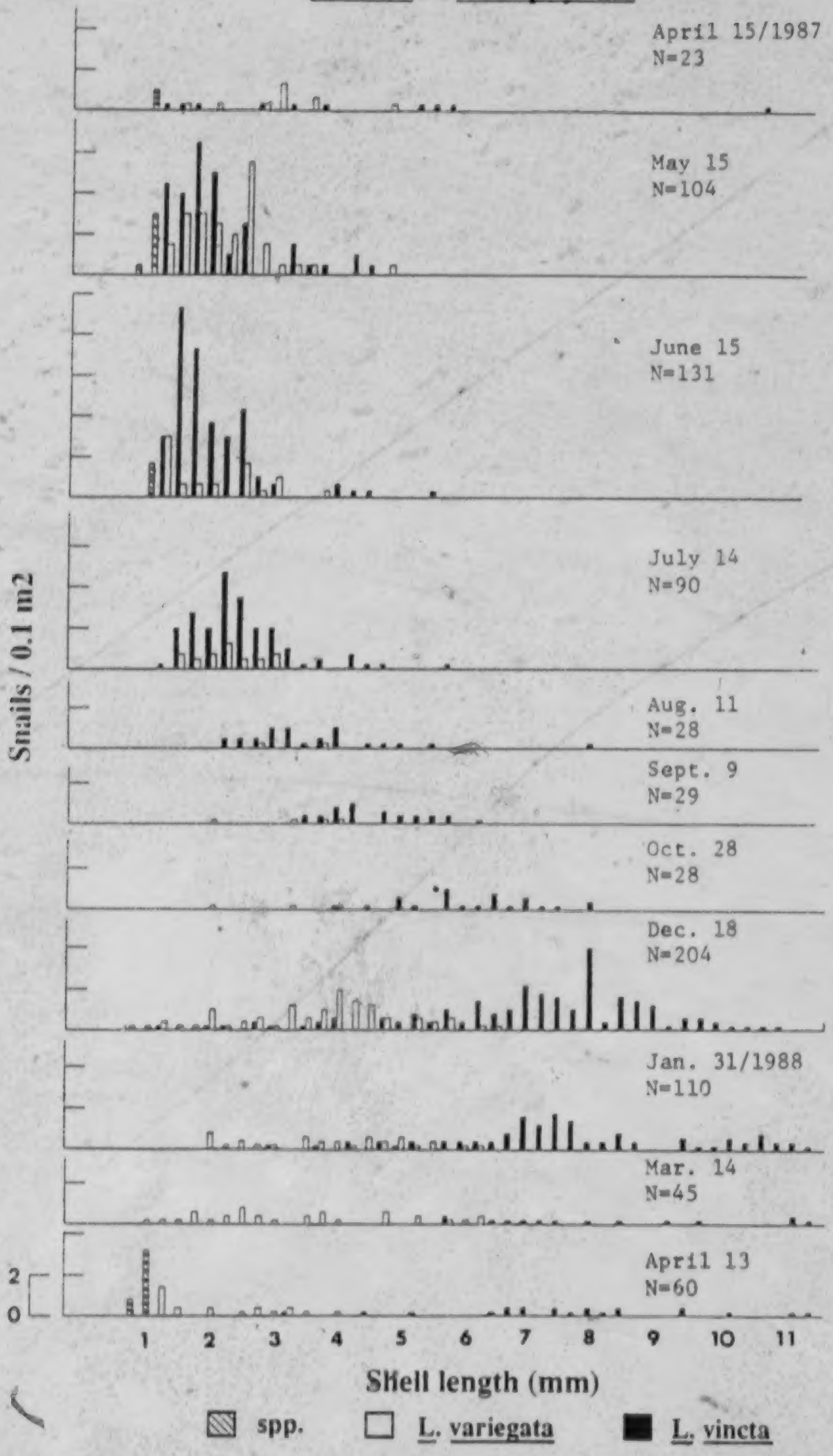


Figure 4.7. B. Size distributions of _Lacuna vincta_, _L. variegata_ and _L_. spp. on _Hedophyllum sessile_ at Prasiola Point from May 04, 1988 through November 23, 1988. Numbers below dates indicate total number of snails in samples.

Lacuna on Hedophyllum

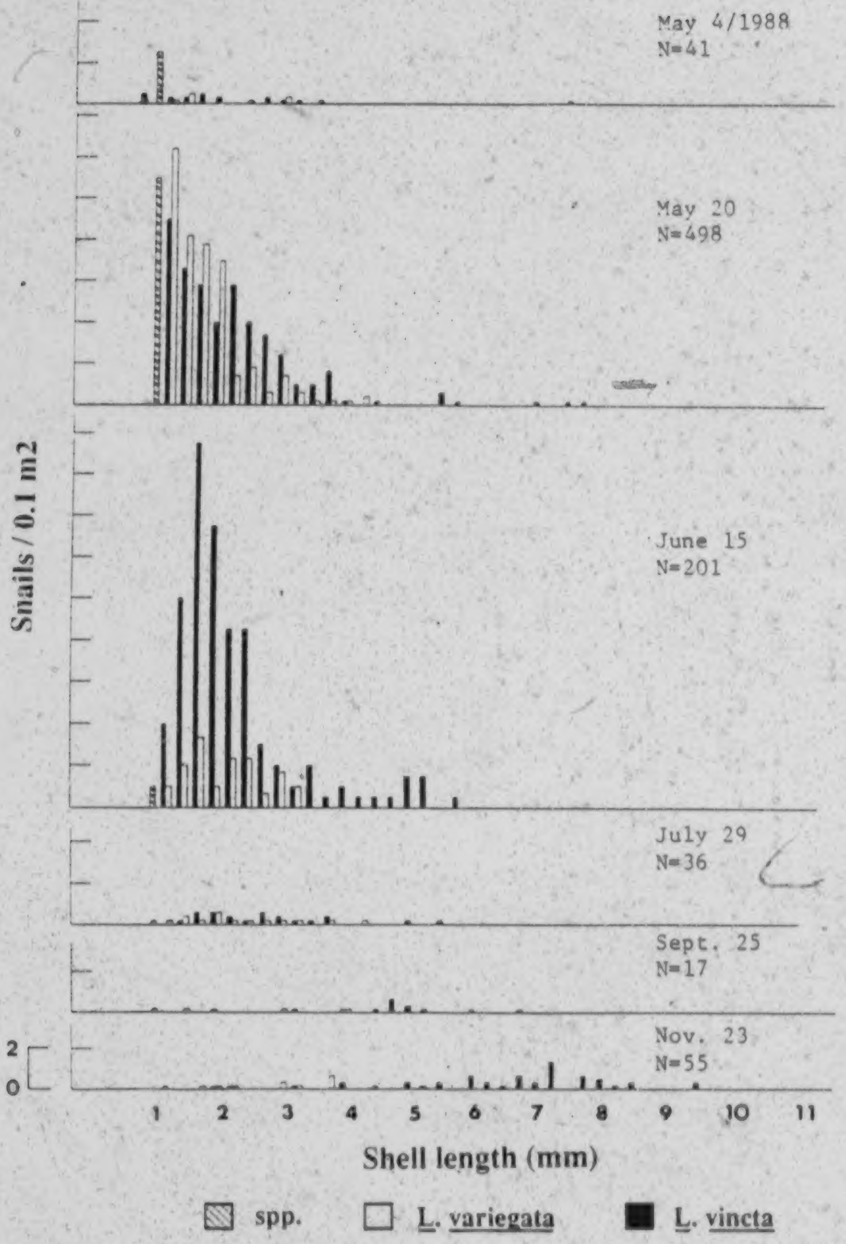
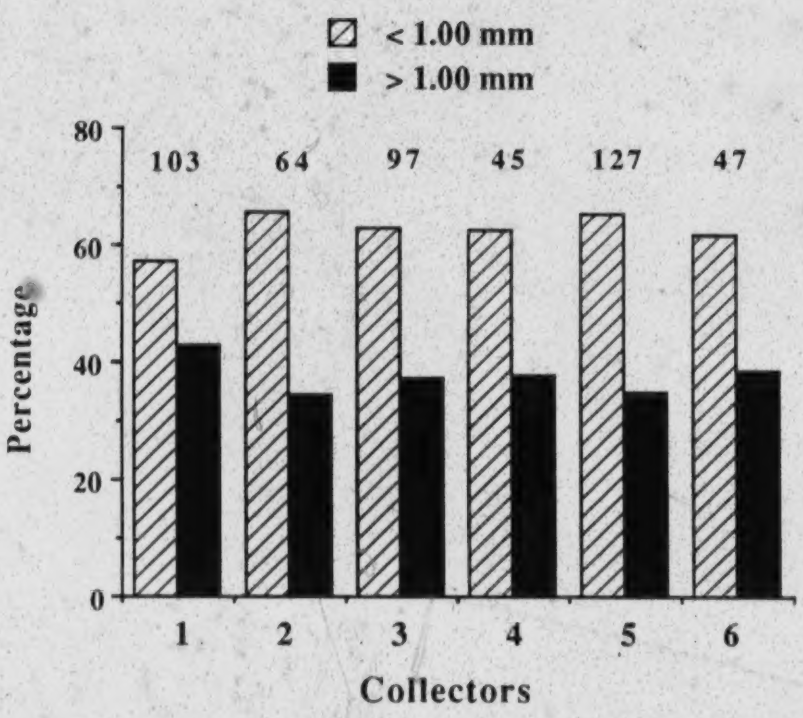


Figure 4.8. Percentage of individual *Lacuna* spp. < or > 1.00 mm caught in six off-bottom *Gracilaria pacifica* collectors installed for 24 hour periods at Prasiola Point between May 04 and May 07, 1988 (during peak larval settlement period). Numbers above histograms represent total number of individuals collected.


▨ < 1.00 mm
■ > 1.00 mm
80
60
40
20
0
Percentage
103
64
97
45
127
47
1
2
3
4
5
6
Collectors

juveniles is conservative and likely underestimates the total number of drifting juveniles (see Fig. 2.11, Chapter II).

The size-frequency distributions of *Lacuna* spp. caught in off-bottom collectors also showed that post-metamorphic drifting occurred year-round (Fig. 4.9; also see Tables 3.1 and 3.2, Chapter III). Results from *Gracilaria* collectors installed during November showed that mostly *L. variegata* were drifting at that time of the year (one *L. vincta*: shell length = 3.7 mm). During November, *L. variegata* between 2 and 4 mm shell length were common in collectors (Fig. 4.9 D).

Significantly larger individual *Lacuna* spp. were found in collectors made of flat *Hedophyllum* blades than in those made of *Gracilaria* (*Hedophyllum* collectors: mean shell length = 1.484 mm, SD = 0.695, n = 122; *Gracilaria* collectors: mean 1.174 mm, SD = 0.523, n = 253) (Mann-Whitney 2 Sample Test, Z = 4,665, p < 0.001) (Fig. 4.9 A, B). Only 40.7% of the *Lacuna* spp. found in the *Hedophyllum* collectors had shell length < 1 mm, compared to 58.9% for those found in *Gracilaria* collectors (Fig. 4.9 A, B). This suggests that larval settlement occurred at a lower rate on *Hedophyllum* than on structurally-complex algae like *Gracilaria*. Moreover, the average number of *Lacuna* spp. (all sizes) caught in the *Gracilaria* collectors was up to seven times higher than that of *Hedophyllum* collectors, with 65.05 and 8.36 individuals / collector / day, respectively (Mann-Whitney 2 Sample Test, Z = 3.963, p < 0.001) (Fig. 4.10).

Figure 4.9. Size-frequency distributions of *Lacuna vincta*, *L. variegata* and *L.* spp. caught in two types of off-bottom intertidal collectors at Prasiola Point during three seasons (1988). A) *Gracilaria pacifica* collectors: May. B) *Hedophyllum sessile* collectors: May. C) *G. pacifica* collectors: August. D) *G. pacifica* collectors: November.

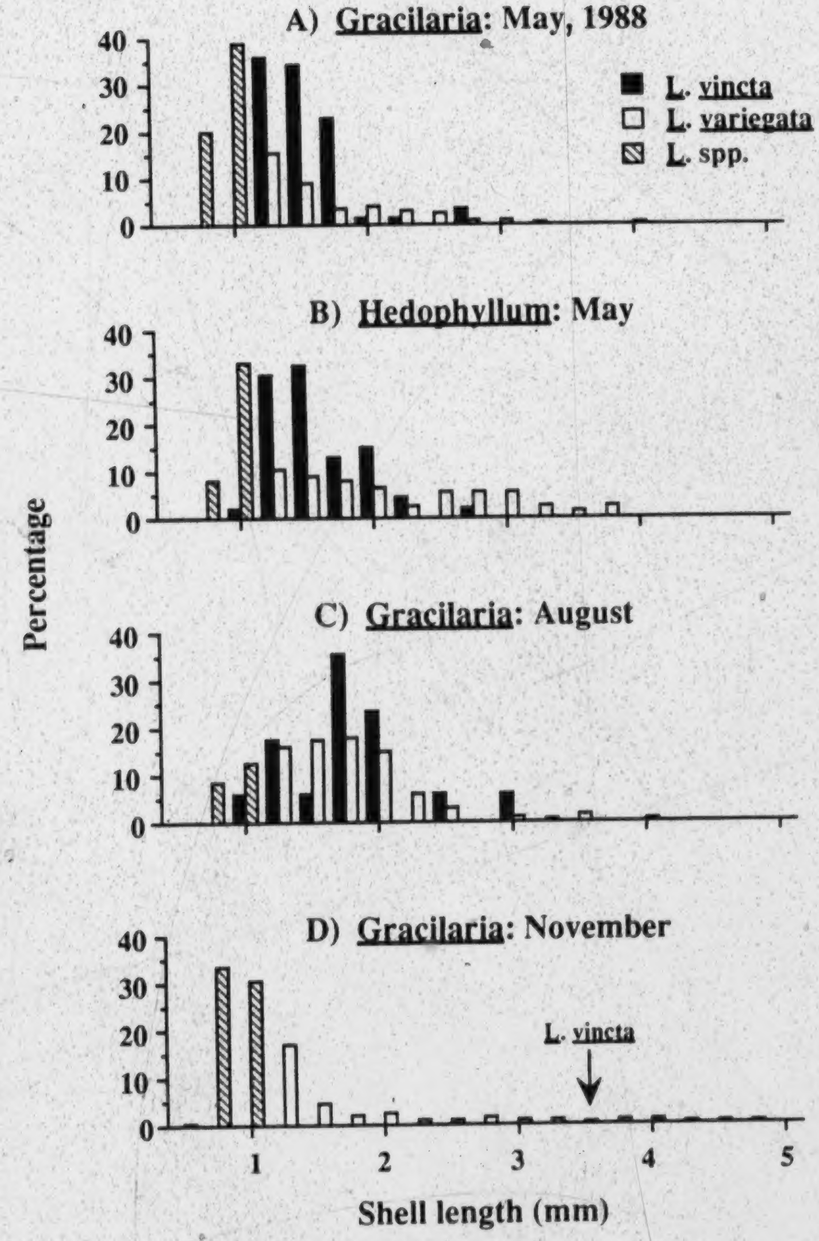
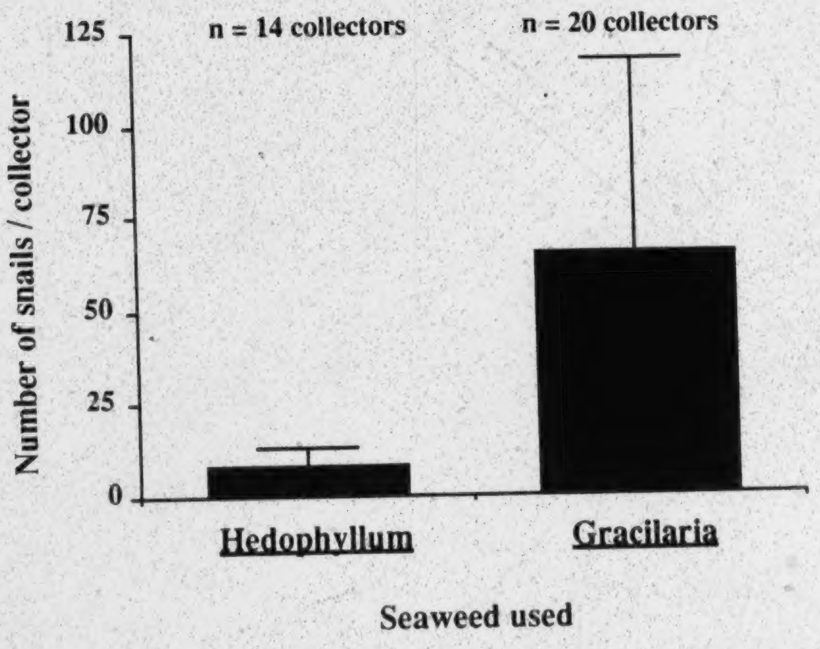

A) Gracilaria: May, 1988
■ L. vincta
☐ L. variegata
▨ L. spp.
B) Hedophyllum: May
C) Gracilaria: August
D) Gracilaria: November
L. vincta
Percentage
40
30
20
10
0
1
2
3
4
5
Shell length (mm)

Figure 4.10. Comparison between the number of _Lacuna_ spp. found in _Hedophyllum sessile_ and _Gracilaria pacifica_ collectors in 24 hours periods during May 1988.


n = 14 collectors
n = 20 collectors
Number of snails / collector
125
100
75
50
25
0
Hedophyllum
Gracilaria
Seaweed used

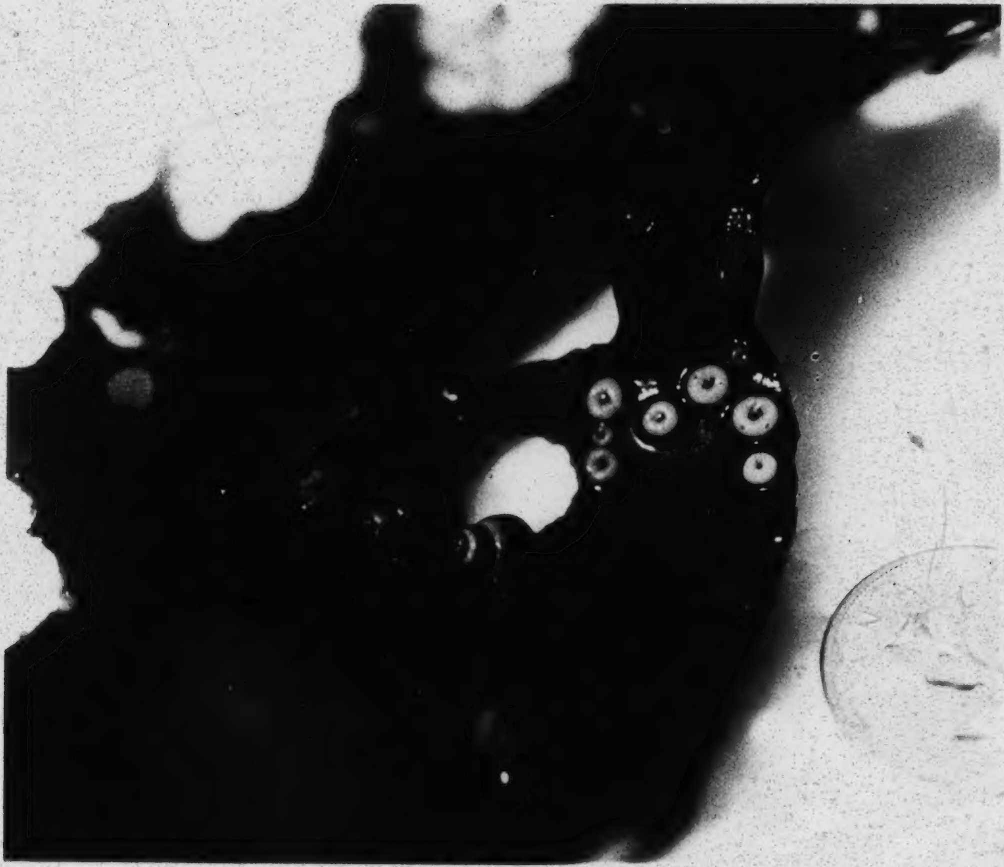
c. Growth and lifespan of Lacuna vincta on Hedophyllum

Analysis of size-frequency distributions of individuals found on Hedophyllum at Prasiola Point suggests that the growth of Lacuna vincta was slow during late spring/early summer but increased rapidly during late summer/fall (Fig. 4.7 A, B). Between July and December, the growth was steady at 1.0-1.5 mm per month. The distinct bimodal size distribution observed in the samples of January 1988 was due to the sexual dimorphism occurring in L. vincta (Fig. 4.7 A). At that time, the average size of sexually mature males was 6.72 mm (SD = 1.235 mm, n = 43), while that of females was 8.79 mm (SD = 2.057 mm, n = 38) (Fig. 4.7 A). January corresponded to the beginning of the main spawning period (Fig. 4.11), thus 7-8 months after peak recruitment.

Although large numbers of juvenile Lacuna variegata occurred in the pits and bullae of Hedophyllum blades during early spring/summer, for unknown reasons the number of individuals of this species decreased during the fall and winter, leaving L. vincta as the dominant species in the habitat at the time of reproduction (winter) (Fig. 4.7).

Peak recruitment occurred during the spring and was followed by rapid growth during late summer/fall. Most Lacuna vincta were sexually mature during the winter and peak egg-laying period occurred during January/April (Fig. 4.11; also see Fig. 2.2, Chapter II). During April/early May, most adults had disappeared from the Hedophyllum habitat and were presumably dead (Fig. 4.7).

Figure 4.11. Two adult Lacuna vincta and their egg masses on Hedophyllum sessile at Prasiola Point (spring 1988). Note the small size of the snails compared with the coin.



3. Abundance and size-frequency distributions of Lacuna spp. in the turf algal community

Contrary to the delay observed between the timing of larval settlement and the arrival of new recruits on *Hedophyllum*, recruitment of *Lacuna* spp. in the red turf algal community and period of larval settlement were synchronous (Fig. 4.12). A significant increase in density of snails occurred between mid-April and the first week of May of 1988 (Mann-Whitney 2 Sample Test, $Z = 2.459$, $p < 0.02$) (Fig. 4.12) and coincided with the presence of numerous advanced *Lacuna* spp. veligers in the plankton (see Fig. 2.5, Chapter II). The average density of newly-metamorphosed *Lacuna* spp. in the turf algal communities during the spring/summer was one order of magnitude higher than that observed on *Hedophyllum* during the same period (Fig. 4.12; compare with Fig. 4.2), with up to 666 individuals per 0.1 m^2 during July 1988 ($SD = 216.4$, $n = 5$ quadrats). However, this period of high abundance of *Lacuna* spp. in the turf algae was followed by a marked decrease during the fall (July-November: Kruskal-Wallis ANOVA, $H = 9.251$, $p < 0.01$) (Fig. 4.12), coinciding with a drop in the biomass of seaweeds (Fig. 4.1).

Analysis of size-frequency distributions showed that only small juvenile *Lacuna* spp. (0.75-2.75 mm shell length) occurred in the turf community (modes: 1.00-1.50 mm) (Fig. 4.13). In addition, size-frequency distributions of *Lacuna* spp. found in *Gracilaria* collectors and those of individuals found in the turf algae were similar (Figs. 4.9, 4.13).

Figure 4.12. Seasonal abundance of Lacuna spp. on red turf algae at Prasiola Point in 1988. Points show mean number of snails per of 0.1 m^2 quadrat (0.317 X 0.317 m). Numbers in parenthesis indicate total number of snails in all samples. Error bars represent ± SD.

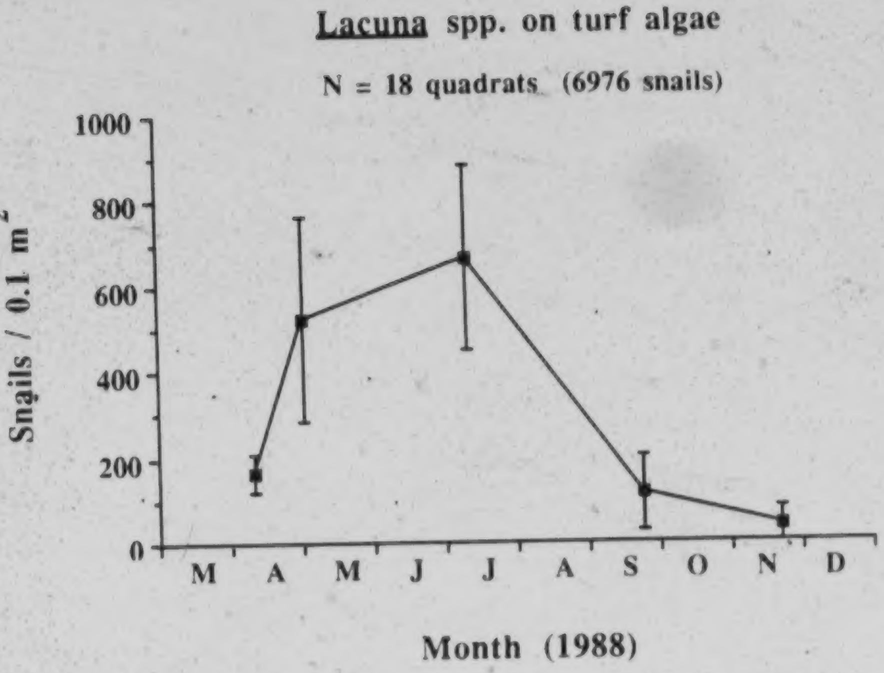
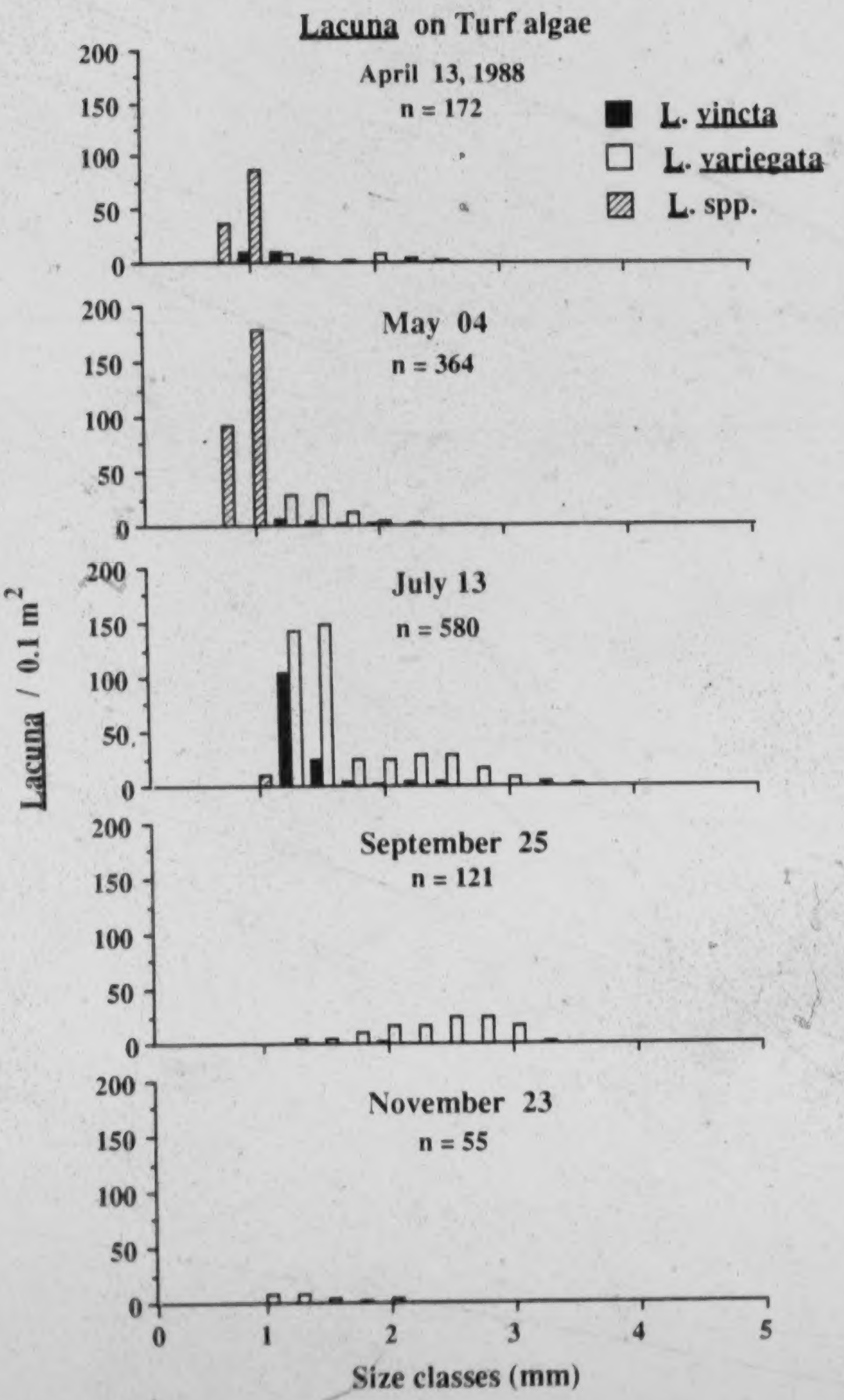

Lacuna spp. on turf algae
N = 18 quadrats (6976 snails)
1000
800
600
400
200
0
Snails / 0.1 m2
M
A
M
J
J
A
S
O
N
D
Month (1988)

Figure 4.13. Size distributions of _Lacuna_ _vincta_, _L._ _variegata_ and _L._ spp. on red turf algae at Prasiola Point during 1988. Bars show mean number of individuals of each size-class per 0.1 m^2 quadrat (0.317 m X 0.317 m). Numbers below dates indicate total number of snails in quadrats (4-7 quadrats / month).


Lacuna on Turf algae
April 13, 1988
n = 172
■ L. vincta
□ L. variegata
▨ L. spp.
May 04
n = 364
July 13
n = 580
September 25
n = 121
November 23
n = 55
200
150
100
50
0
0
1
2
3
4
5
Lacuna / 0.1 m²
Size classes (mm)

Thus, high settlement rates of *Lacuna* spp. larvae in the turf algal community indicate that these structurally-complex microhabitats represent an important substratum used by larvae as well as by newly-metamorphosed juvenile *Lacuna* spp. (Figs. 4.12, 4.13).

4. Evidence of winter immigration of large juvenile and adult *Lacuna vincta* to the *Hedophyllum* community

A comparison of population dynamics of *Lacuna vincta* on *Hedophyllum* and on *Halosaccion* patches during late fall/winter indicated a reciprocal relationship in the pattern of abundance of these snails in these two algal communities (Fig. 4.14). During that time (before and during egg laying period) when densities of *L. vincta* on *Hedophyllum* increased, densities of snails on *Halosaccion* decreased to reach near zero values (Kruskal-Wallis ANOVA, $H = 10{,}66$; $p < 0{,}02$) (Figs. 4.14, 4.15; see also Figs. 4.2 and 4.7). The analysis of size-frequency distributions indicated that large juvenile and adult *L. vincta* were immigrating to *Hedophyllum* (Fig. 4.14) (which had flat blades at that time; see Figs. 4.3, 4.4 A). Thus, these findings suggest that the increase in *L. vincta* density on *Hedophyllum* was the result of immigration (crawling or drifting) of large individuals from other surrounding seaweeds, like the *Halosaccion* community.

Figure 4.14. Comparison of the abundances and the size distributions of Lacuna vincta on Halosaccion glandiforme and Hedophyllum sessile at Prasiola Point from September 1987 through January 1988. Histograms show mean number of L. vincta of each size class per 0.1 m^2 quadrat (0.317 X 0.317 m). A) H. glandiforme. B) H. sessile. Note the reciprocal pattern of abundance of snails between the two seaweeds. Numbers below dates indicate total numbers of snails in quadrats (4-7 quadrats / month / plant).

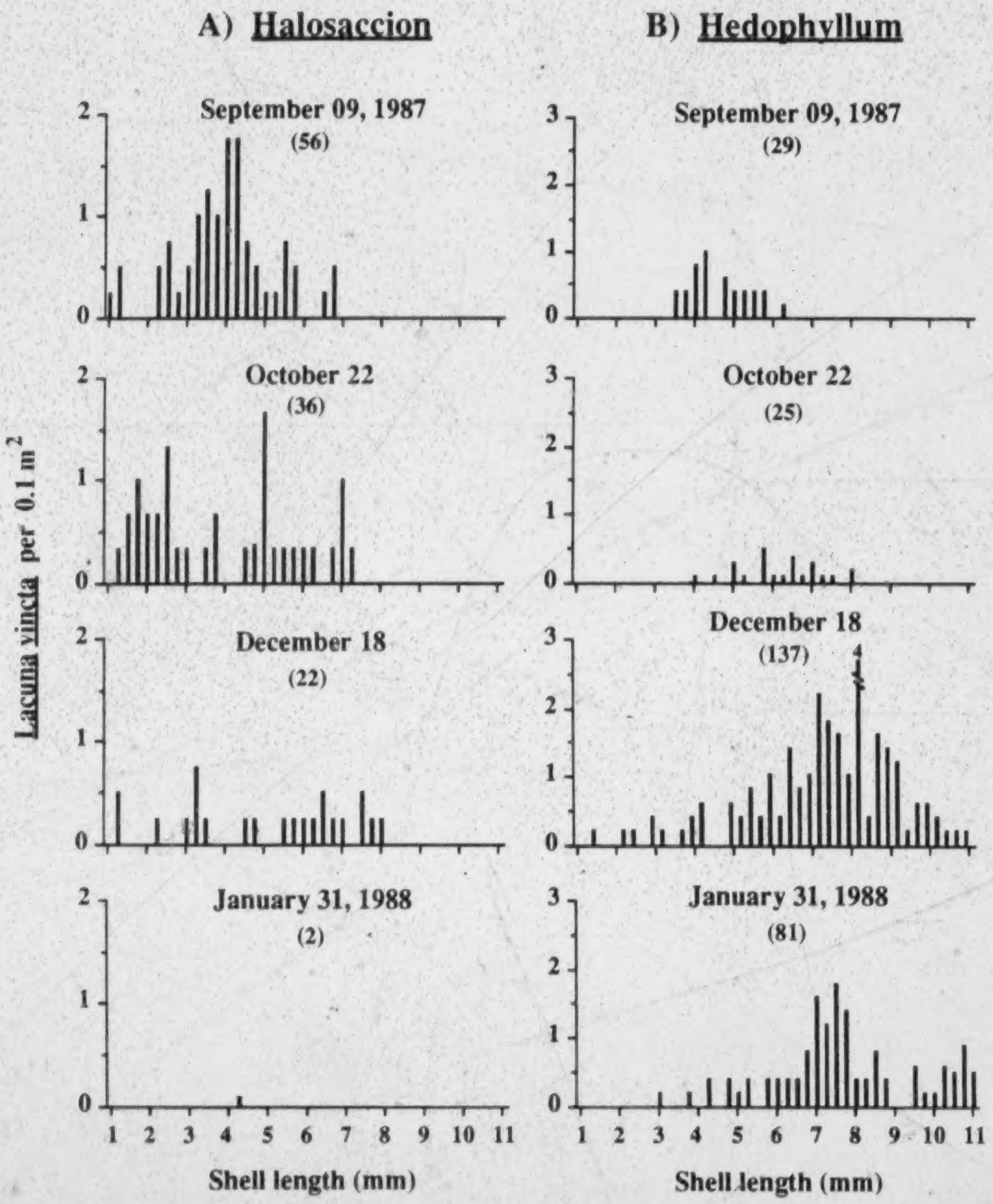
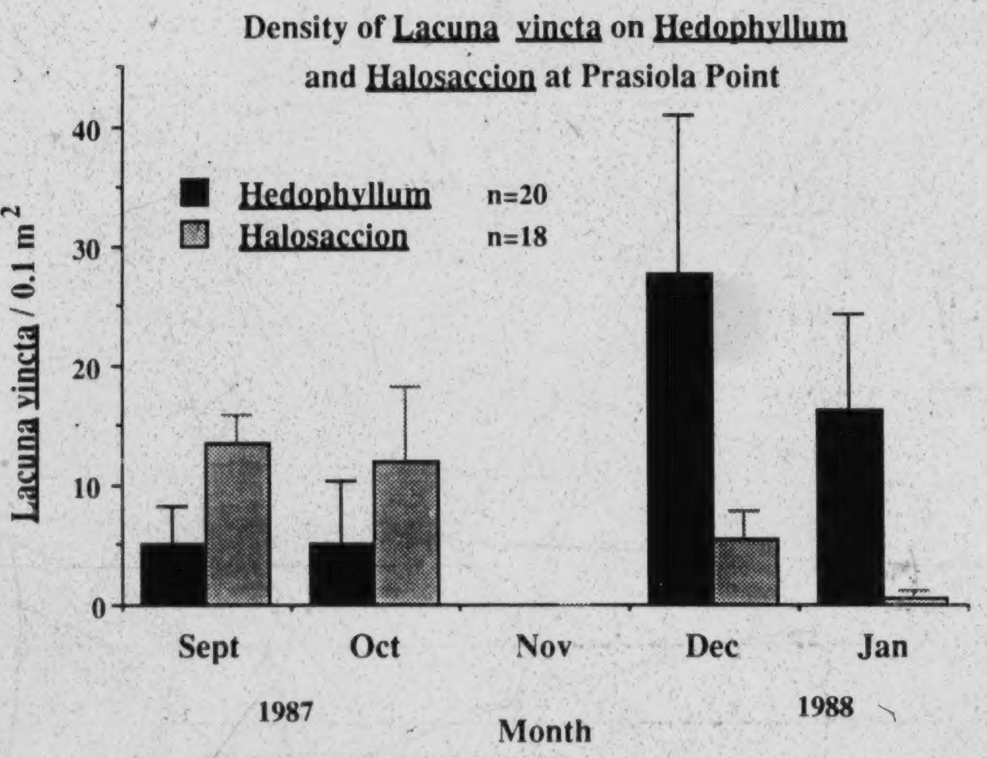

A) Halosaccion
B) Hedophyllum
September 09, 1987
(56)
(29)
October 22
(36)
(25)
December 18
(22)
(137)
4
January 31, 1988
(2)
(81)
Lacuna vincta per 0.1 m2
0
1
2
3
1 2 3 4 5 6 7 8 9 10 11
Shell length (mm)

Figure 4.15. Comparison between the abundances of *Lacuna vincta* on *Halosaccion glandiforme* and *Hedophyllum sessile* at Prasiola Point from September 1987 through January 1988. Note the reciprocal pattern of abundances of snails between the two seaweeds. Histograms show mean number of *L. vincta* per 0.1 m^2 quadrat (4-7 quadrats / month / plant). Error bars represent ± SD.



Density of Lacuna vincta on Hedophyllum and Halosaccion at Prasiola Point

5. Abundance and size-frequency distributions of Lacuna spp. on the red alga Iridaea

The phenomenon of bullation observed on *Hedophyllum* does not occur on *Iridaea*, a red alga with a thin (but tough) rubbery blade. The annual pattern of abundance of *Lacuna* spp. on *Iridaea* also differed from that observed on *Hedophyllum* (Fig. 4.16; compared with Fig. 4.2). During the first year of this study, abundance of snails on *Iridaea* reached a peak during late fall/early winter, with densities increasing from about 20 *Lacuna* spp. / 0.1 m^2 during early summer of 1987 to 190 individuals / 0.1 m^2 during December of 1987 (Kruskal-Wallis, $H = 11.39$, $p < 0.02$) (Fig. 4.16). Abundance of snails fell to low values during late spring/early summer of 1988 as they did during April/June of 1987. The abnormally high density of snails in the samples of July 1988, were likely due to the presence of turf algae inside the *Iridaea* quadrats (Fig. 4.16). Finally, the density of snails on *Iridaea* increased from September through November of 1988 (Mann-Whitney 2 Sample Test, $Z = 2.731$, $p < 0.01$).

The increases in density of *Lacuna* spp. on *Iridaea* that occurred during the fall of 1987 and the fall of 1988 were related to the arrival of snails of various size classes (Fig. 4.17 A, B, C). During these periods, individuals of shell length < 1 mm represented only a small proportion of the total number snails recruiting to *Iridaea*. Moreover, individual *L. variegata* of practically all size classes

Figure 4.16. Seasonal abundance of Lacuna spp. on Iridaea cordata at Execution Rock during 1987 and 1988. Points show mean number of snails per 0.1 m^2 quadrat (0.317 m X 0.317 m) (4-7 quadrats / month). Error bars represent ± SD.

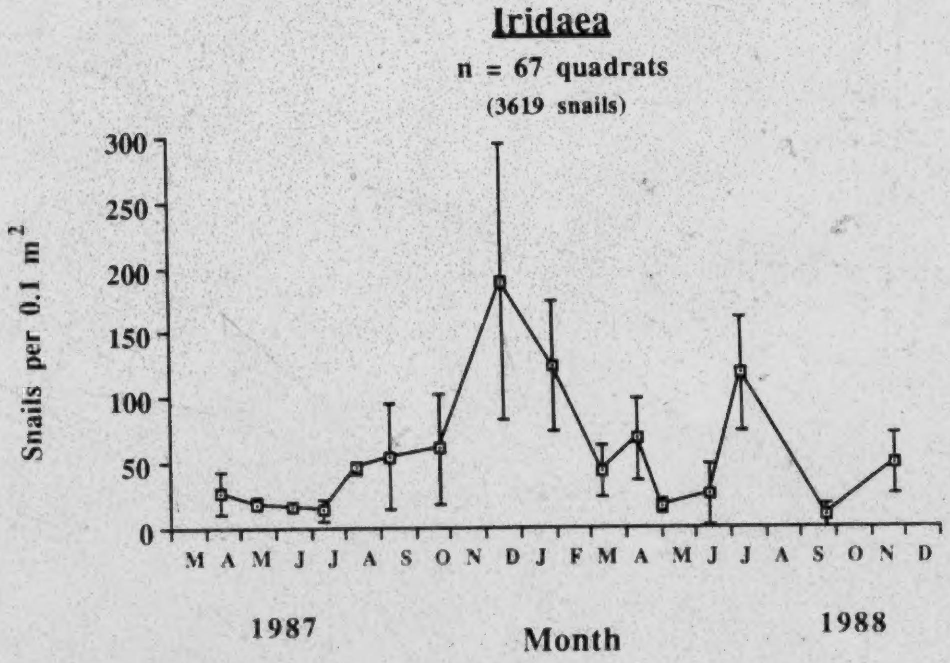

Iridaea
n = 67 quadrats
(3619 snails)
Snails per 0.1 m²
300
250
200
150
100
50
0
M A M J J A S O N D J F M A M J J A S O N D
1987
Month
1988

Figure 4.17. **A.** Size distributions of Lacuna vincta, L. variegata and L. spp. on Iridaea cordata at Execution Rock from April 15, 1987 through December 18, 1987. Histograms show mean number of individuals of each size-class per 0.1 m^2 quadrat (0.317 m X 0.317 m) (4-7 quadrats / month). Numbers below dates indicate total number of snails in samples (cont'd).

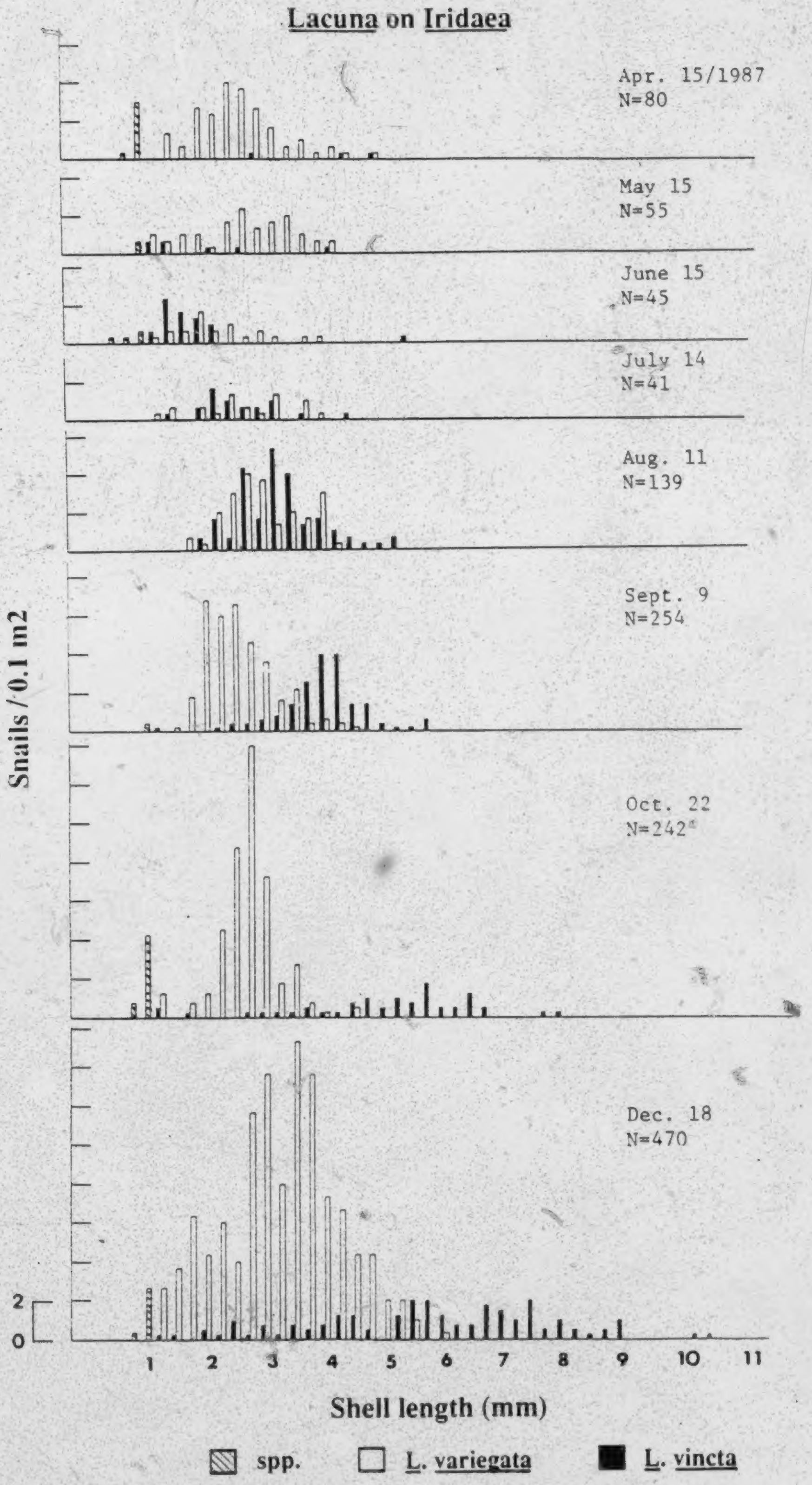

Lacuna on Iridaea
Apr. 15/1987
N=80
May 15
N=55
June 15
N=45
July 14
N=41
Aug. 11
N=139
Sept. 9
N=254
Oct. 22
N=242
Dec. 18
N=470
Snails / 0.1 m2
2
0
1
2
3
4
5
6
7
8
9
10
11
Shell length (mm)
▨ spp.
☐ L. variegata
■ L. vincta

Figure 4.17. B. Size distributions of *Lacuna vincta*, *L. variegata* and *L.* spp. on *Iridaea cordata* at Execution Rock from January 31, 1988 through June 15, 1988. Histograms show average number of individuals of each size-class per 0.1 m^2 quadrat (0.317 X 0.317 m) (4-7 quadrats / month). Numbers below dates indicate total number of snails in samples.

Lacuna on Iridaea

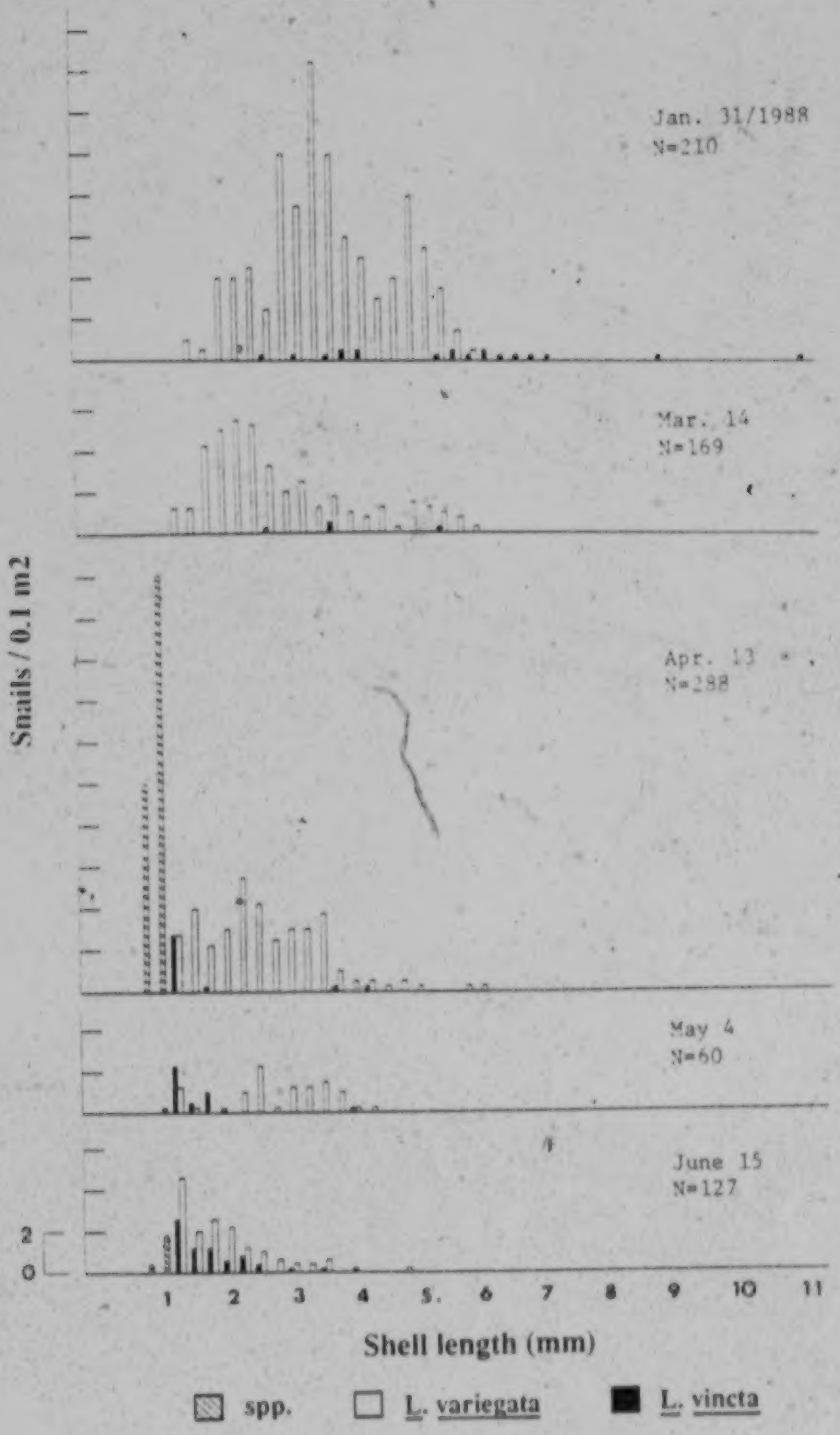
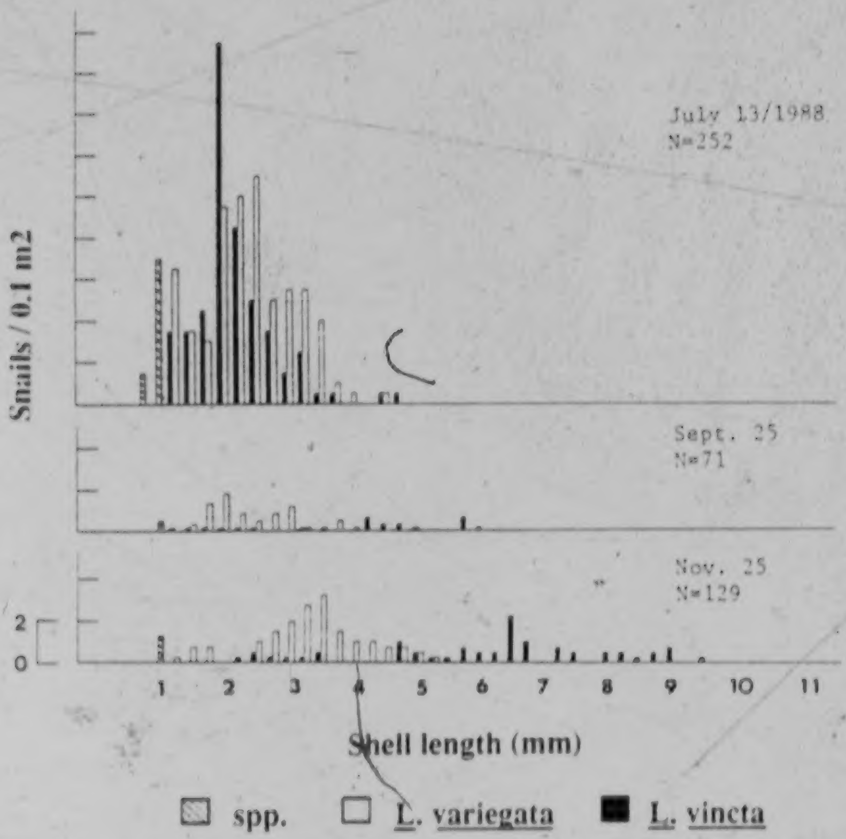


Figure 4.17. C. Size distributions of _Lacuna vincta_, _L. variegata_ and _L._ spp. on _Iridaea cordata_ at Execution Rock from July 13, 1988 through November 25, 1988. Histograms show average number of individuals of each size-class per 0.1 m^2 quadrat (0.317 m X 0.317 m) (4-7 quadrats / month). Numbers below dates indicate total number of snails in samples.

Lacuna on Iridaea



occurring on Iridaea have been found in off-bottom collectors during the summer and fall (Fig. 4.9).

The analysis of size-frequency distributions of Lacuna variegata on Iridaea showed that this snail grows more slowly and reaches sexual maturity at smaller sizes than does L. vincta (Figs. 4.17 A, B, C).

During the winter, while abundance of snails on Iridaea was at its maximum, egg masses of Lacuna variegata were also abundant on the plant (see Fig. 2.2, Chapter II). L. variegata sampled during spawning (January, 1988) showed a bimodal distribution, with a distinct mode at 3.5 mm and another at 5.0 mm, representing adult males and females, respectively (males: mean = 3.29 mm, SD = 0.593, n = 98; females: mean = 4.33 mm, SD = 1.100, n = 85) (Fig. 4.17 B).

The abundance of the different size classes of the two species of Lacuna on Iridaea showed that, although L. vincta was common, L. variegata dominated this seaweed (Fig. 4.17 A, B, C). The reverse was true of Hedophyllum (Fig. 4.7 A, B). These differences in abundance reflect differences in interspecific habitat preferences between the two species of snails. The dominance of L. vincta on Hedophyllum and of L. variegata on Iridaea was also observed in the San Juan Islands and in other areas of southern Vancouver Island.

6. Effect of diet on growth and fecundity in Lacuna variegata

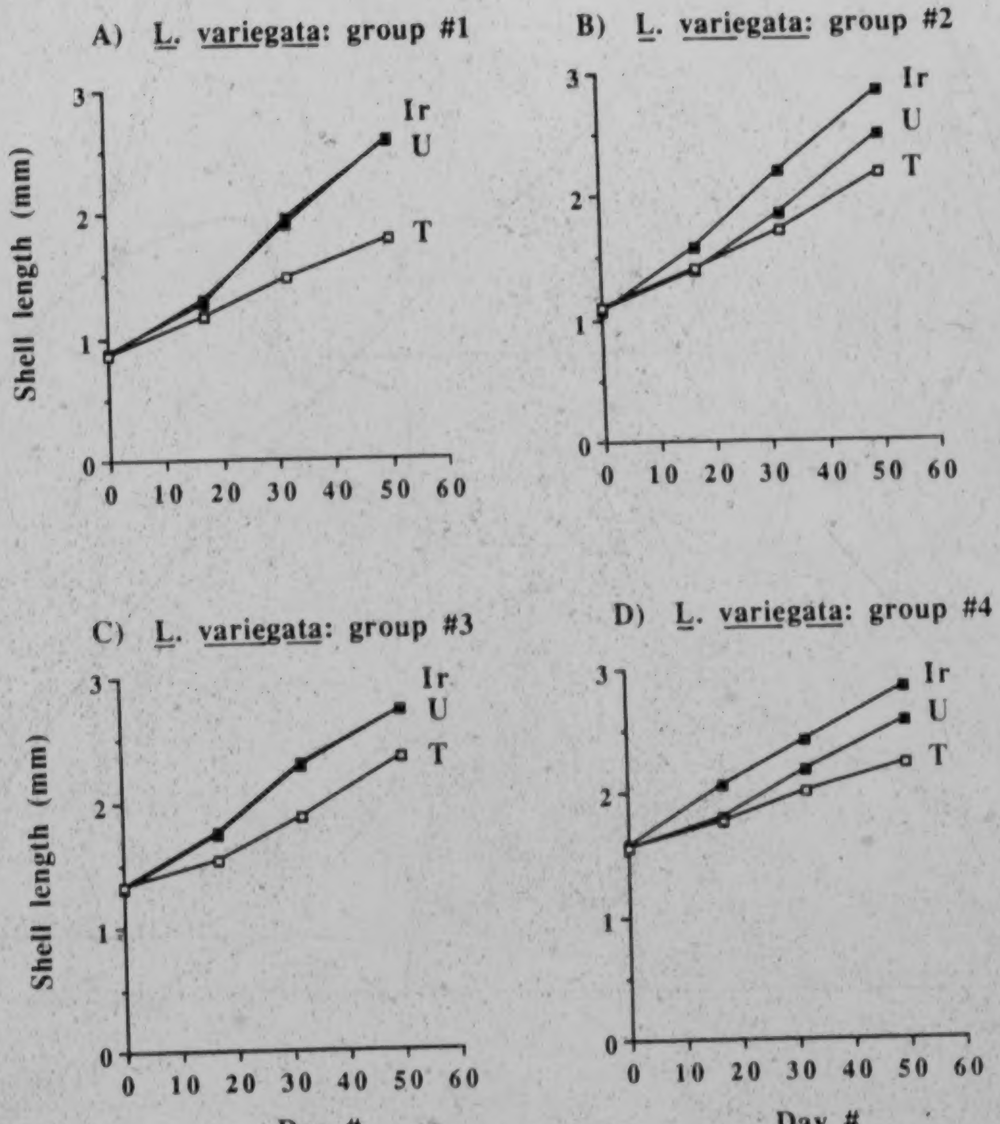
a. Growth

Four size-groups of Lacuna variegata were raised in the laboratory on three intertidal seaweeds. Results showed that the type of alga on which L. variegata grows and feeds has a marked effect on growth rates (ANCOVA; for each size-group, differences among slopes and means are significant; $p < 0.05$) (Fig. 4.18). When raised on Iridaea, growth rates of L. variegata were highest. Growth rates of L. variegata on Iridaea were, from the smallest to the largest size-group: group A = 1.08 mm / month, B = 1.12 mm / month, C = 0.97 mm / month and D = 0.84 mm / month (Fig. 4.18). These growth rates were 78-87% higher than those of snails raised on the turf alga Odonthalia, a seaweed on which L. variegata larvae settle heavily. On this alga, average monthly growth rates were: group A = 0.61 mm, B = 0.62 mm, C = 0.54 mm and D = 0.45 mm (Fig. 4.18). Fecal pellet examination during the experiments confirmed that juveniles were indeed eating the algae placed in the dishes.

b. Fecundity

Lacuna variegata raised on Iridaea deposited more egg masses after 33 days than did those raised on the other two seaweeds (Kruskal-Wallis ANOVA, H = 8.5097, $p < 0.025$). On day 50, snails raised on Iridaea and Ulva had deposited egg masses that were 1.75-2.58 times larger (area of egg mass disk) than those from snails raised on Odonthalia (group C: H

Figure 4.18. Growth of four size-groups (1, 2, 3, 4) of juvenile *Lacuna variegata* on three intertidal algae found at Prasiola Point. Ir = *Iridaea cordata*, U = *Ulva lactuca*, T = *Odonthalia floccosa*. Points show mean shell length (mm) after 17, 33 and 50 days of growth. Note lower growth rates when juveniles were raised on *O. floccosa*.



A) L. variegata: group #1

B) L. variegata: group #2

C) L. variegata: group #3

D) L. variegata: group #4

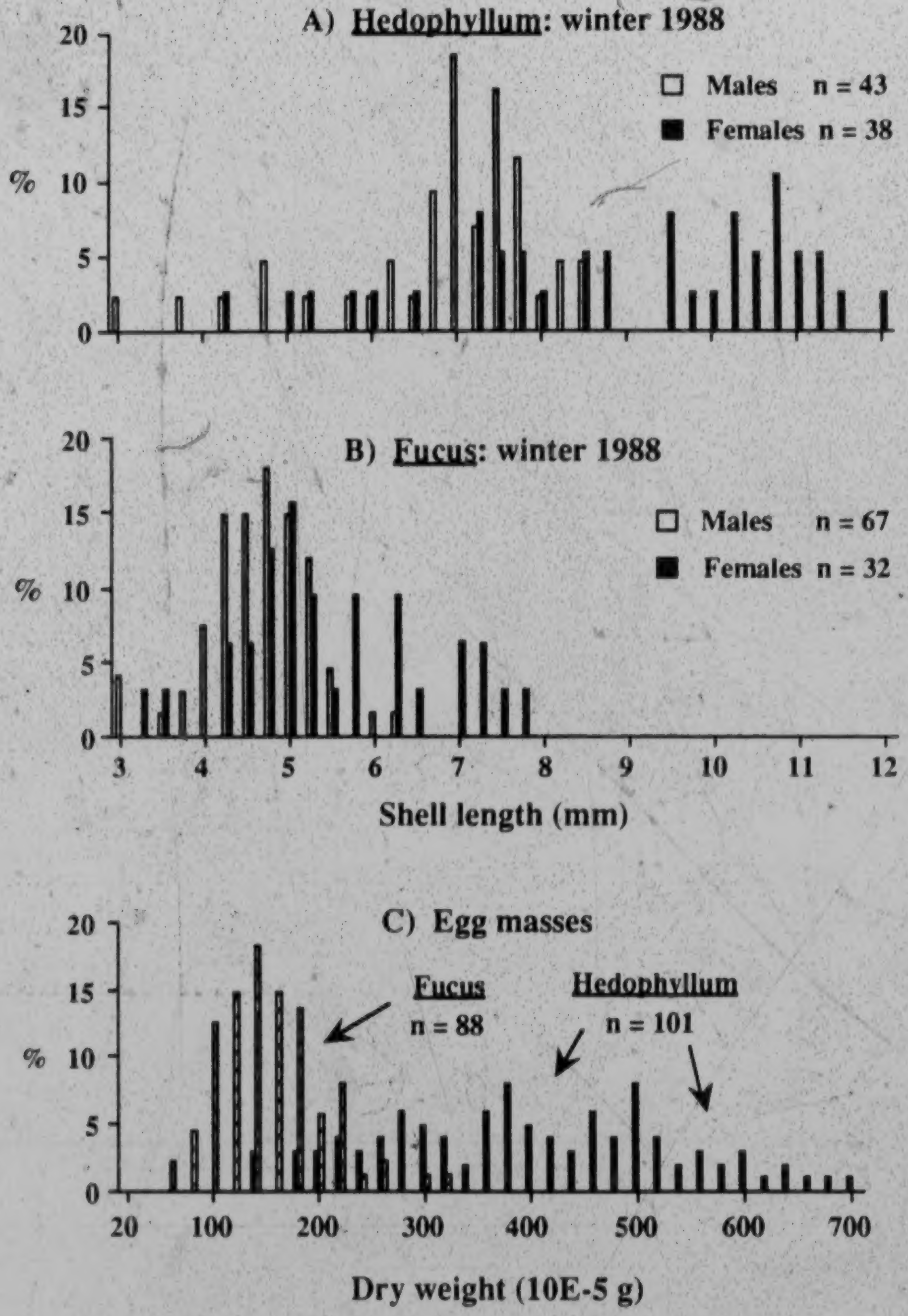
= 8.24, $p < 0.025$; group D: $H = 19.17$, $p < 0.001$).

7. Field evidence of habitat-related differences in adult size, sexual dimorphism and size of egg masses in *Lacuna vincta*

The average size of adult males and females between populations of *Lacuna vincta* living in different habitats during the breeding period (January-March) differed significantly (Fig. 4.19 A, B). Sexually mature male *L. vincta* living on *Hedophyllum* at Prasiola Point had an average shell length 50.6% larger than that of males living on *Fucus* in Grappler Inlet (*Hedophyllum*: 6.715 mm, SD = 1.235, n = 43; *Fucus*: 4.459 mm, SD = 0.731, n = 67; Mann-Whitney 2 Sample Test: $Z = -7.392$, $p < 0.001$) (Fig. 4.19 A, B). The size difference in females between the two habitats was even greater, with sexually mature females on *Hedophyllum* 63.6% larger than those on *Fucus* in Grappler Inlet (*Hedophyllum*: mean = 8.793 mm, SD = 2.057, n = 38; *Fucus*: mean = 5.375 mm, SD = 1.121, n = 32; $Z = -5,949$, $p < 0.001$) (Fig. 4.19 A, B).

Sexual dimorphism, as well, was more pronounced in *Lacuna vincta* found on *Hedophyllum* (Prasiola Point) than in individuals living on *Fucus* (Grappler Inlet) (Fig. 4.19 A, B). The difference between the average size (shell length) of males and that of females for *L. vincta* on *Hedophyllum* was as high as 2.08 mm, or 30.9%, compared to only 0.92 mm, or 20.5% for *L. vincta* living on *Fucus* (Fig. 4.19 A, B).

Figure 4.19. Comparison of adult sizes, sexual dimorphism and dry weights of egg masses in Lacuna vincta between two seaweeds. A, B) Size-frequency distributions of adult male and female L. vincta from Hedophyllum sessile (Prasiola Point) and Fucus disticus (Grappler Inlet) during the peak of the breeding season. C) Distribution of dry weights of L. vincta's egg masses from females living on H. sessile (Prasiola Point) and on F. disticus (Grappler Inlet). Numbers indicate sample size.


A) Hedophyllum: winter 1988
☐ Males n = 43
■ Females n = 38
%
0
5
10
15
20
B) Fucus: winter 1988
☐ Males n = 67
■ Females n = 32
%
0
5
10
15
20
3
4
5
6
7
8
9
10
11
12
Shell length (mm)
C) Egg masses
Fucus
n = 88
Hedophyllum
n = 101
%
0
5
10
15
20
20
100
200
300
400
500
600
700
Dry weight (10E-5 g)

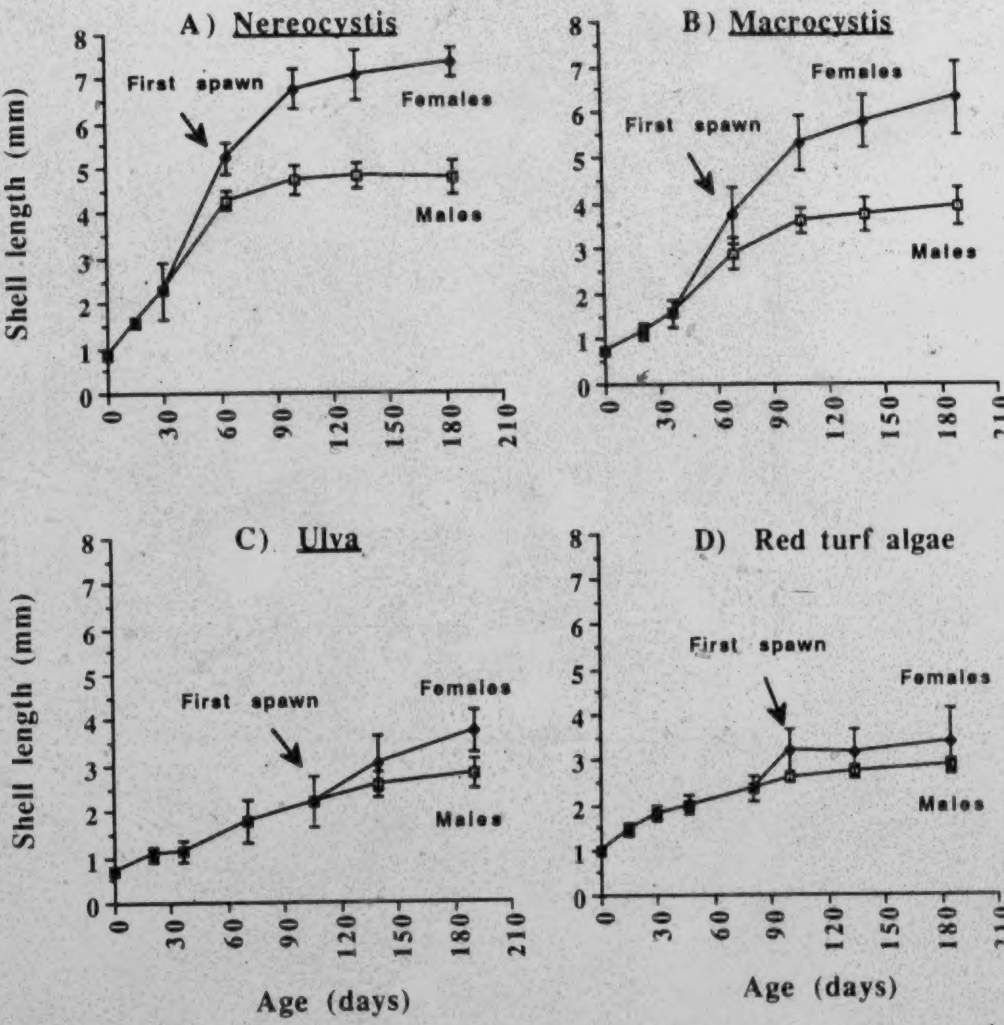
Female *Lacuna vincta* on *Hedophyllum* at Prasiola Point deposited egg masses that were, on average, 2.67 times larger than those from females living on *Fucus* (*Hedophyllum*: mean dry weight = 385 X 10^{-5} g, SD = 143.2, n = 102; *Fucus*: mean = 143.8 X 10^{-5} g, SD = 49.7, n = 88) (Mann-Whitney 2 Sample Test, Z = -10.995, $p < 0.001$) (Fig. 4.19 C).

8. Long-term effects of substratum choice on growth rates, size and lifetime fecundity in *Lacuna vincta*: Series I (newly-metamorphosed juveniles to adults)

a. Growth rates and adult size

When newly-metamorphosed juvenile *Lacuna vincta* of 0,75-0,90 mm (for red turf algae: 0.95-1.08 mm) were raised on seaweeds -- *Nereocystis*, *Macrocystis*, red turf algae (see Materials and Methods for list of species) and *Ulva* -- differences in growth rates, size of adults as well as sexual dimorphism were observed (Fig. 4.20). Growth rates were highest on *Nereocystis* and *Macrocystis*, with female *L. vincta* reaching 7.33 mm and 6.33 mm, and males 4.76 mm and 3.93 mm at the age of six months (Fig. 4.20 A, B). Lowest growth rates were observed in snails raised on *Ulva* and red turf algae; average size of females was only 3.76 mm and 3.41, and that of males 2.86 mm and 2.82, respectively, at the age of six months (Kruskal-Wallis ANOVA, comparison between the four diets; males: H = 21.70, $p < 0.001$; females: H = 17.28, $p < 0.001$) (Fig. 4.20 C, D).

Figure 4.20. Growth of newly-metamorphosed Lacuna vincta on four intertidal algae. A) Nereocystis luetkeana (n = 18). B) Macrocystis integrifolia (n = 33 snails). C) Ulva lactuca (n = 18). D) Red turf algae (3 species; see Materials and Methods) (n = 30). Points show mean shell lengths (mm). Error bars represent ± SD.


A) Nereocystis
B) Macrocystis
C) Ulva
D) Red turf algae
Shell length (mm)
Age (days)
First spawn
Females
Males
0
1
2
3
4
5
6
7
8
0
30
60
90
120
150
180
210

Lacuna vincta raised on Macrocystis and Nereocystis reached sexual maturity at a larger size and started breeding earlier (age at first spawn: 64-70 days), than those raised on Ulva and turf algae (age at first spawn: 100-124 days) (Fig. 4.20). A distinct sexual dimorphism occurred in those that grew on kelp, with females 54-61% larger than males (Fig. 4.20 A, B). In contrast, sexual dimorphism was less pronounced when L. vincta were raised on Ulva and red turf algae (females 19-33% larger than males) (Fig. 4.20 C, D).

b. Effects of type of seaweed on lifetime fecundity

Fecundity was noticeably affected by the type of seaweeds on which Lacuna vincta fed (Fig. 4.21). Females between three and six months of age that were raised on Nereocystis or Macrocystis deposited 4-9 times more egg masses / month (average cumulative number of 18.0-19.8 egg masses / female) than did those raised on red turf algae or Ulva (average cumulative number of 2.4-3.7 egg masses / female) (egg masses / month: Kruskal-Wallis ANOVA, $H = 44.00$, $p < 0.001$) (Fig. 4.21 A, B). In addition, the average dry weight of egg masses deposited by females raised on Macrocystis and Nereocystis was 3 or 4 times higher than that of females raised on the turf algae or Ulva (One-way ANOVA: $F = 12.094$, $p < 0.001$) (Fig. 4.21 C).

To estimate lifetime fecundity a regression equation relating the number of eggs and dry weight of egg masses was calculated (Fig. 4.22) ($r^2 = 0.9409$; $F = 597.1$; $p < 0.001$) (see Fig. 4.23 for summary). Female L. vincta raised on kelp

Figure 4.21. Lifetime reproductive ouptut of *Lacuna vincta* when raised on four intertidal algae. Ner: *Nereocystis luetkeana*; Mac: *Macrocystis integrifolia*; Reds: 3 species of red turf algae (see Materials and Methods); Ulva: *Ulva lactuca*. A) Number of egg masses per female per month (t = 0: n = 49 females). B) Cumulative number of egg masses per female. C) Average dry weight (10^{-5} g) of egg masses from females raised on the four different algae (Ner: n = 22 egg masses; Mac: n = 75; Reds: n = 3; Ulva: n = 18). Error bars represent ± SD.

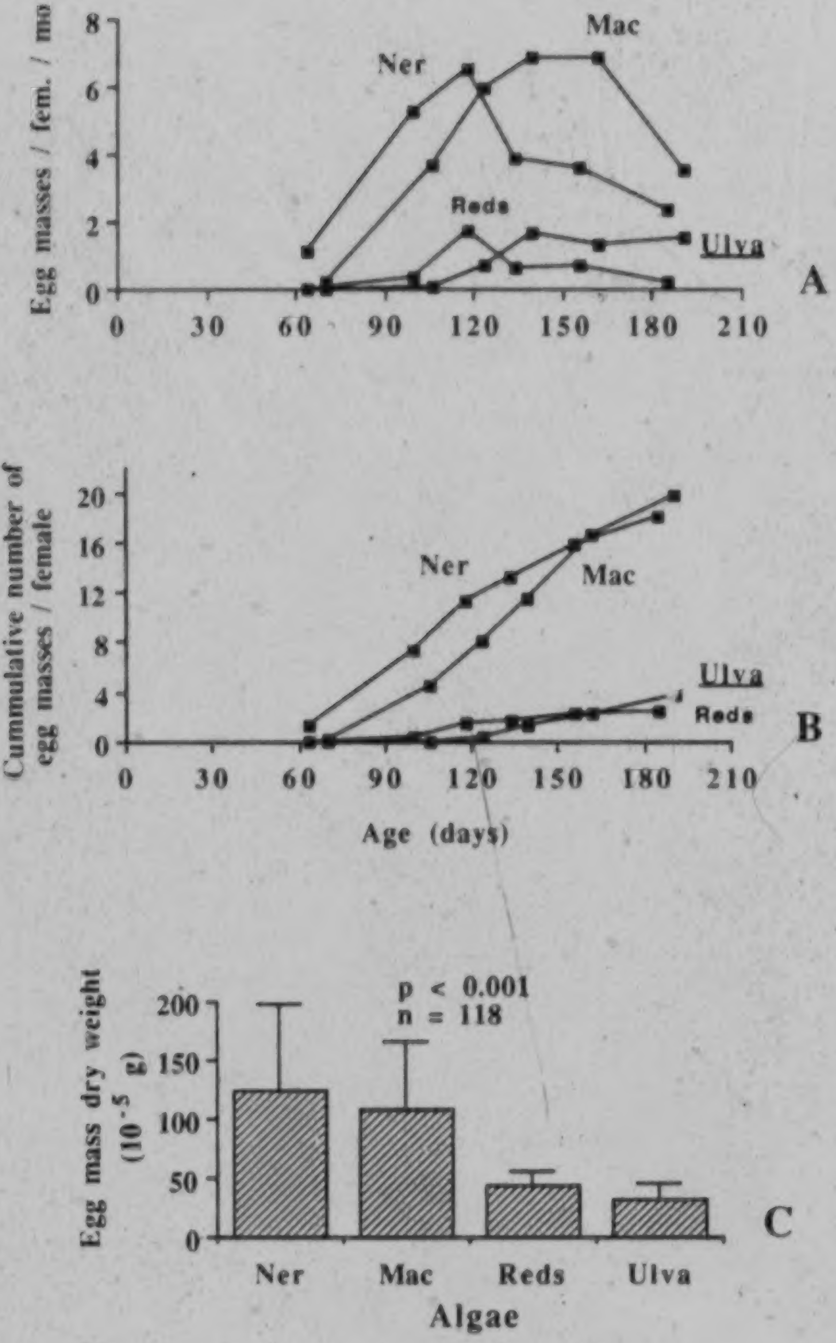

Egg masses / fem. / mo
8
6
4
2
0
Ner
Mac
Reds
Ulva
0
30
60
90
120
150
180
210
A
Cummulative number of egg masses / female
20
16
12
8
4
0
Ner
Mac
Ulva
Reds
0
30
60
90
120
150
180
210
Age (days)
B
Egg mass dry weight (10^{-5} g)
200
150
100
50
0
p < 0.001
n = 118
Ner
Mac
Reds
Ulva
Algae
C

Figure 4.22. Relationship between number of eggs and dry weight of Lacuna vincta egg masses. Regression equation shown above.

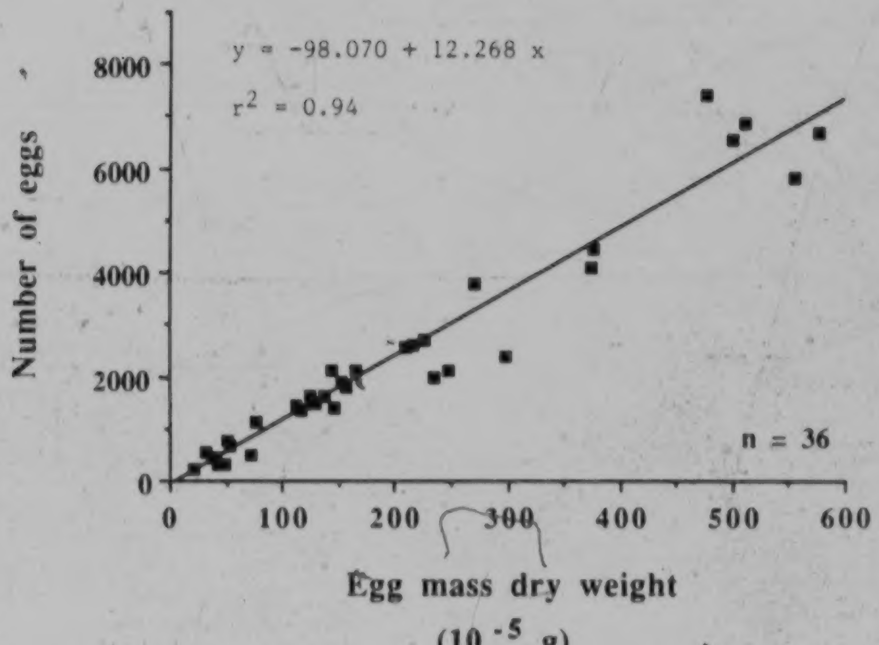
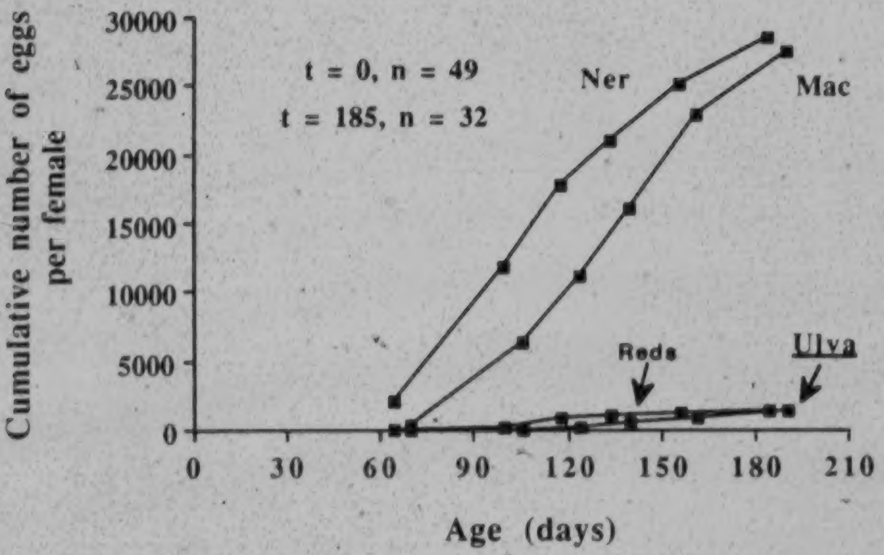

y = -98.070 + 12.268 x
r^2 = 0.94
n = 36
Number of eggs
8000
6000
4000
2000
0
0
100
200
300
400
500
600
Egg mass dry weight
(10 -5 g)

Figure 4.23. Lifetime fecundity of *Lacuna vincta* raised on four intertidal algae (expressed as cumulative number of eggs deposited by female). Ner: *Nereocystis luetkeana*; Mac: *Macrocystis integrifolia*; Reds: 3 species of red turf algae (see Materials and Methods); Ulva: *Ulva lactuca*.


Cumulative number of eggs per female
30000
25000
20000
15000
10000
5000
0
t = 0, n = 49
t = 185, n = 32
Ner
Mac
Reds
Ulva
0
30
60
90
120
150
180
210
Age (days)

produced an average of 27,000-29,000 eggs, while those on red turf algae and Ulva, deposited ten times less eggs (< 2500 eggs) during the same interval (Fig. 4.23). At the age of 6-7 months, 70-80% of the snails had died. Many of the remaining females continued to lay eggs, albeit at a reduced rate, suggesting that they were capable of producing more eggs than the above calculated values. Their maximum lifespan on kelp in the laboratory was 6-9 months.

9. Long-term effects of substratum choice on growth rates, size and lifetime fecundity in Lacuna vincta: Series II (large juveniles to adults)

a. Growth rates and adult size

Juvenile Lacuna vincta raised on five intertidal algae (Hedophyllum, Macrocystis, Fucus, Iridaea, and the red turf alga Odonthalia) showed marked differences in growth rates and adult size for both males (One-way ANOVA, group #1: F = 26.071, p < 0.001; group #2: F = 7.736, p < 0.001) and females (Kruskal-Wallis ANOVA, group #1: H = 59.79, p < 0.001; group #2: H = 45.53, p < 0.001) (Figs. 4.24, 4.25). For both size-groups and sexes tested, Hedophyllum consistently allowed higher growth rates and larger sizes. Odonthalia yielded much lower growth rates (Figs. 4.24, 4.25). In the first size-group, the average size of males (started at 2.72-2.74 mm shell length) raised on Hedophyllum increased by as much as 44.7% after 45 days of growth (mean shell length = 3.951 mm), contrasting with only a 12.2% size

Figure 4.24. Growth of juvenile *Lacuna vincta* raised on five intertidal algae found at Prasiola Point: starting at 2.6-2.8 mm shell length (size-group #1). He: *Hedophyllum sessile*; Ma: *Macrocystis integrifolia*; Fu: *Fucus disticus*; Ir: *Iridaea cordata*; Tu: *Odonthalia floccosa*. A) Males. B) Females. Points show mean shell length (mm) of seven groups of 4-8 individuals each. Error bars represent ± SD.

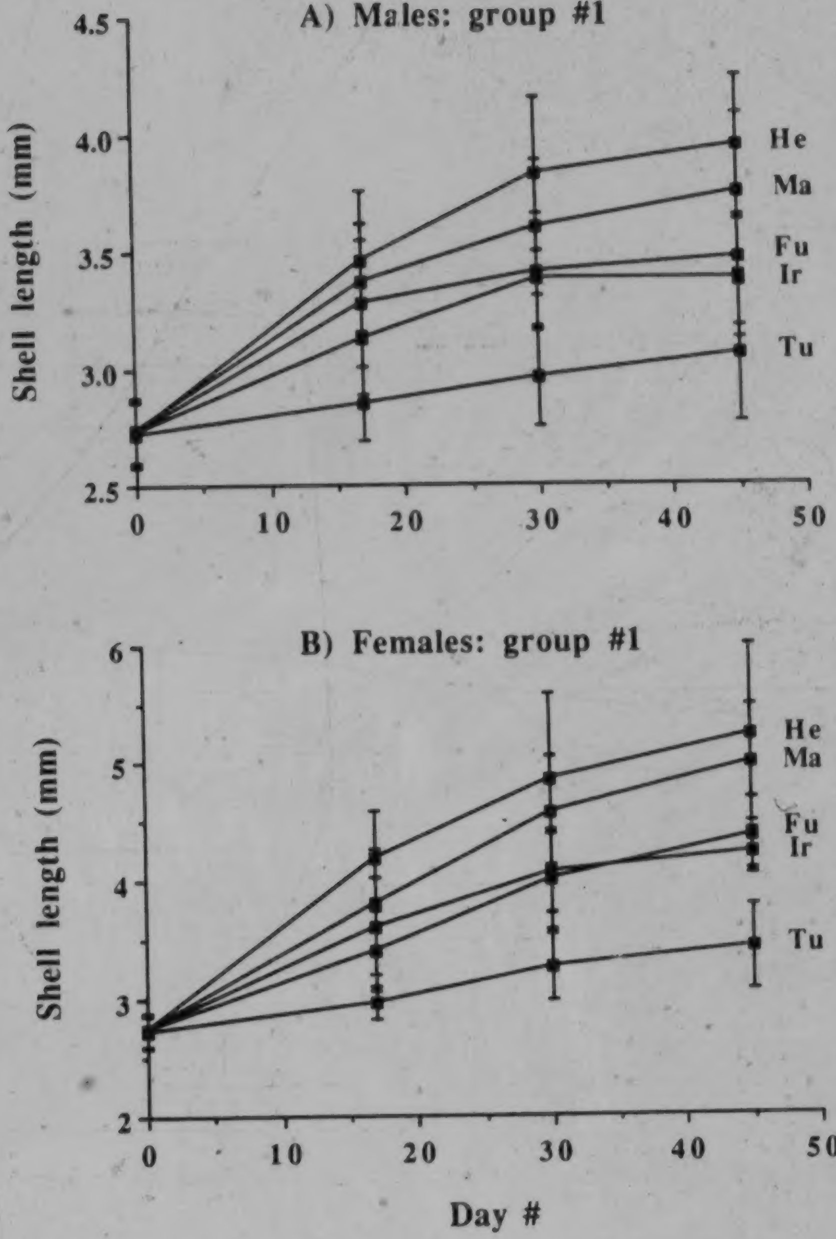
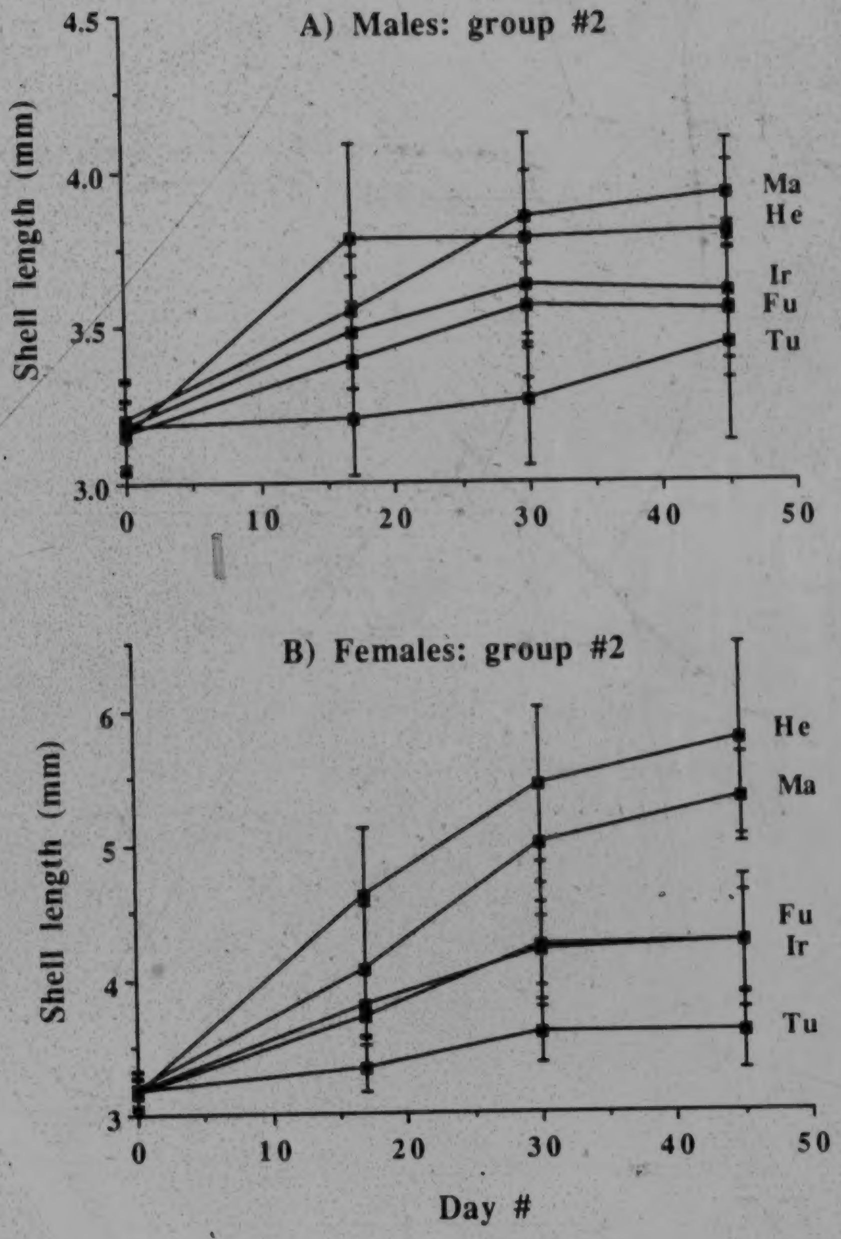

A) Males: group #1
Shell length (mm)
4.5
4.0
3.5
3.0
2.5
0
10
20
30
40
50
He
Ma
Fu
Ir
Tu
B) Females: group #1
Shell length (mm)
6
5
4
3
2
0
10
20
30
40
50
He
Ma
Fu
Ir
Tu
Day #

Figure 4.25. Growth of juvenile *Lacuna vincta* raised on five intertidal algae found at Prasiola Point: starting at 3.15-3.20 mm shell length (size-group #2). He: *Hedophyllum sessile*; Ma: *Macrocystis integrifolia*; Fu: *Fucus disticus*; Ir: *Iridaea cordata*; Tu: *Odonthalia floccosa*. A) Males. B) Females. Points show mean size of 4 groups of 4-8 individuals each. Error bars represent ± SD.


A) Males: group #2
Shell length (mm)
4.5
4.0
3.5
3.0
0
10
20
30
40
50
Ma
He
Ir
Fu
Tu
B) Females: group #2
Shell length (mm)
6
5
4
3
0
10
20
30
40
50
He
Ma
Fu
Ir
Tu
Day #

increase for males raised on the turf alga (mean shell length = 3.063 mm) (Fig. 4.24 A). Similar results were obtained with the second size-group of males (starting at 3.15-3.20 mm), with 20.7% and 8.2% size increase for Hedophyllum and Odonthalia, respectively (Fig. 4.25 A).

Paired multiple comparisons indicated that in the first size-group, males feeding on Hedophyllum reached larger sizes than those feeding on Fucus and Iridaea (Tukey-Kramer, $p < 0.001$) (Fig. 4.24 A). There was a significant difference between the sizes reached on Iridaea and Odonthalia ($p < 0.005$). The differences between male L. vincta raised on Hedophyllum and Macrocystis, and between those raised on Fucus and Iridaea were not significant ($p > 0.05$).

Differences in growth rates between Lacuna vincta raised on the five different seaweeds were more marked in females than in males (Figs. 4.24 B, 4.25 B). On Hedophyllum, the average shell length of female L. vincta at starting sizes identical to those of males increased by as much as 91% and 82.1% in the first and second size-groups, respectively. This markedly contrasted with 24.9% and 12.4% size increase in females raised on Odonthalia (Figs. 24 B, 25 B). Multiple-comparisons analysis for the second size-group revealed that females raised on Hedophyllum grew faster and reached larger sizes than did those raised on Fucus or Iridaea ($p < 0.01$). Females raised on Fucus and Iridaea also showed higher growth rates than those raised on the turf alga (first group, $p < 0.01$) (Fig. 4.25 B).

b. Size-related sexual dimorphism

The type of alga on which *Lacuna vincta* was raised also had a significant effect on the size-related sexual dimorphism (both size-groups) (Kruskal-Wallis ANOVA, $H = 25.35$, $p < 0.001$) (Fig. 4.26). Sexual dimorphism was more pronounced in *L. vincta* raised on *Hedophyllum*, with females as much as 46.4% ($SD = 23.11$, $n = 9$ groups) larger than males (Fig. 4.26). Sexual dimorphism in snails raised on *Fucus* was markedly less pronounced than for females living on *Hedophyllum*, with females 26% ($SD = 8.982$) larger than males (Fig.4.26). A similar situation was observed in the field (see Fig. 4.19 A, B). Sexual dimorphism on *Odonthalia* was the least pronounced, with females only 10.5% ($SD = 7.32$) larger than males, thus a 4.4-fold difference with individuals living on *Hedophyllum* (Fig. 4.26).

c. Spawning rates

For both size-groups, female *Lacuna vincta* raised on *Hedophyllum* were the first to lay egg masses (17 days after the start of the experiments) (Fig. 4.27). The type of seaweed on which *L. vincta* were feeding influenced the rate at which females deposited their egg masses (Kruskal-Wallis ANOVA, group #1: $H = 18.834$, $p < 0.001$; group #2: $H = 11.409$, $p < 0.025$) (Fig. 4.27 A, B). In the first group, after 45 days, females on *Hedophyllum* deposited on average 2.887 egg masses / week, compared with only 0.365 egg mass / week for females raised on *Odonthalia*, thus an 8-fold difference (Fig. 4.27 A).

Figure 4.26. Effect of diet (algae) on the expression of size-related sexual dimorphism in *Lacuna vincta*. Hedo: *Hedophyllum sessile*. Mac: *Macrocystis integrifolia*. Fuc: *Fucus disticus*. Irid: *Iridaea cordata*. Turf: red turf alga *Odonthalia floccosa*. Sexual dimorphism expressed in terms of how much (%) larger (shell length) females are than males. Histograms show mean percentage of 7-9 groups of snails of 4-8 snails each. Error bars represent ± SD.

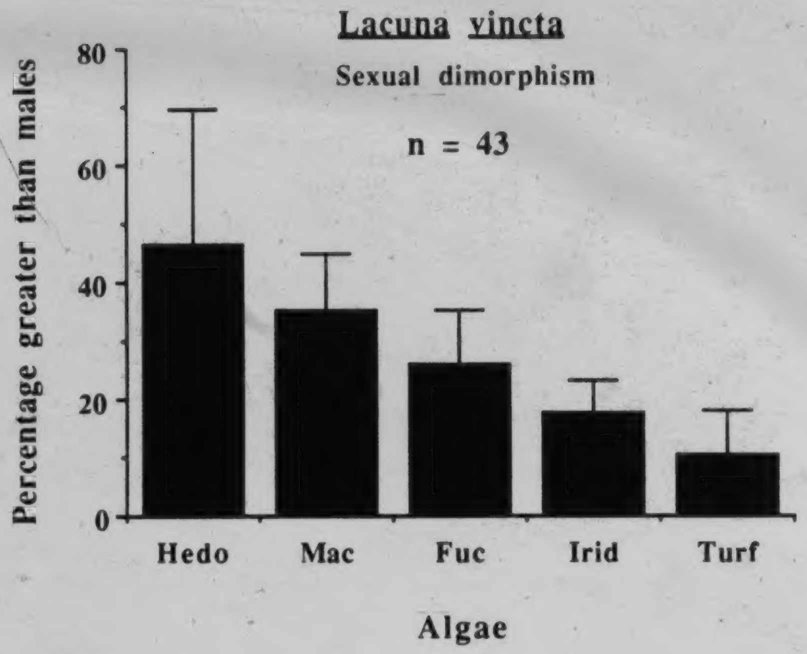
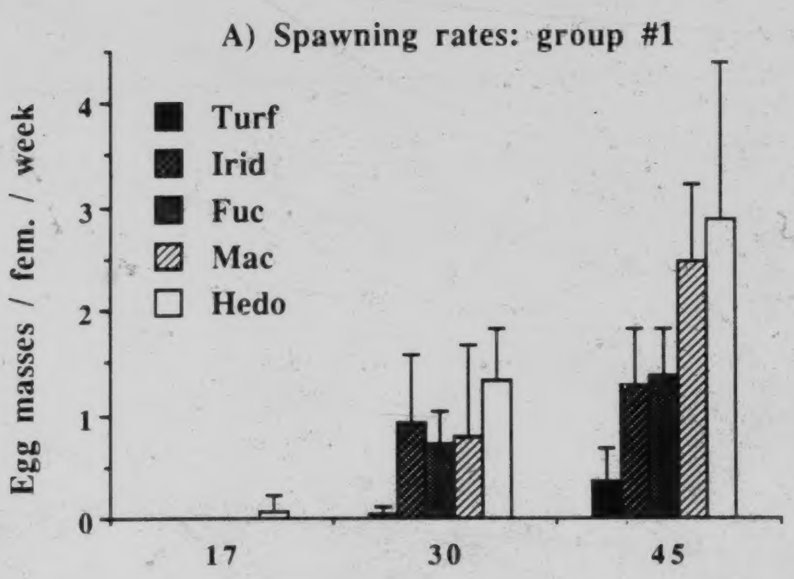
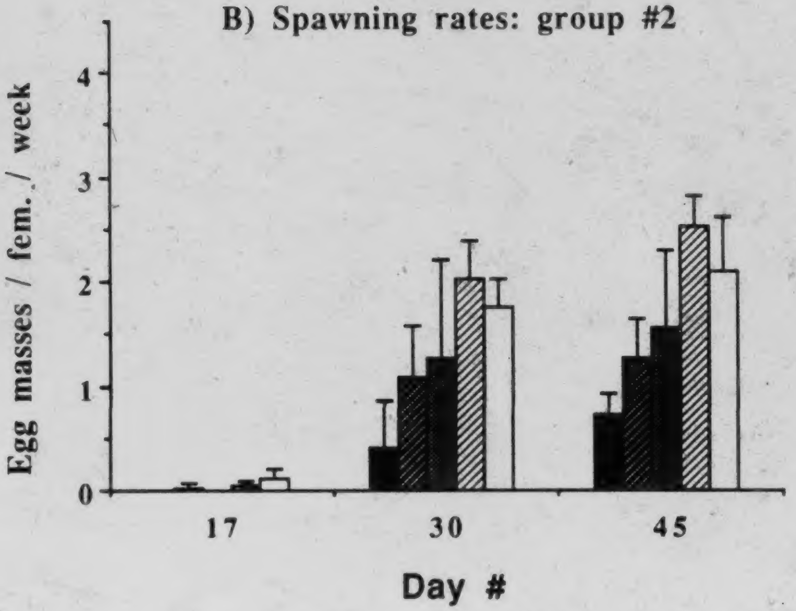

Lacuna vincta
Sexual dimorphism
n = 43
Percentage greater than males
80
60
40
20
0
Hedo
Mac
Fuc
Irid
Turf
Algae

Figure 4.27. Spawning rates (egg masses / female / week) of female *Lacuna vincta* raised on five intertidal algae. Algae: Turf = *Odonthalia floccosa*; Irid: *Iridaea cordata*; Fuc: *Fucus disticus*; Mac: *Macrocystis integrifolia*; Hedo: *Hedophyllum sessile*. A) Size-group #1 (see Material and Methods). B) Size-group #2. Histograms show mean spawning rates of seven (size-group #1) or four (size-group #2) groups of 1-6 individuals each. Error bars represent ± SD.


A) Spawning rates: group #1
Egg masses / fem. / week
0
1
2
3
4
■ Turf
▩ Irid
■ Fuc
▨ Mac
□ Hedo
17
30
45


B) Spawning rates: group #2
Egg masses / fem. / week
0
1
2
3
4
17
30
45
Day #

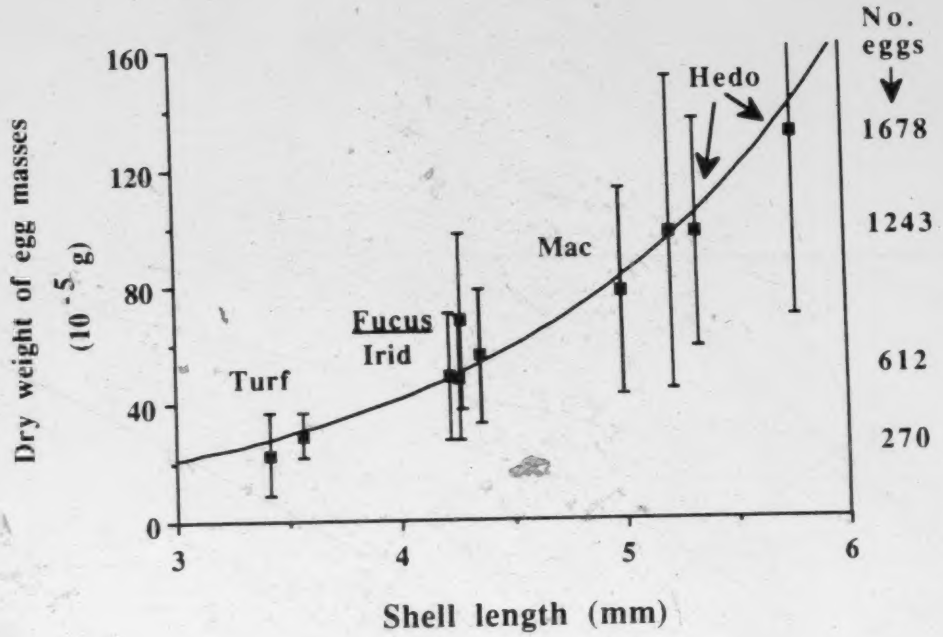
d. Dry weight of *Lacuna vincta* egg masses

There was a 4-fold difference in average dry weight of egg masses of female *Lacuna vincta* raised on five seaweeds after 45 days (Kruskal-Wallis ANOVA, size-group #1: $H = 93.17$, $p < 0.001$; size-group #2: $H = 115.01$, $p < 0.001$) (Fig. 4.28). The largest egg masses were consistently deposited by females that had been feeding on *Hedophyllum* (average dry weight = 97.51 and 131×10^{-5} g for the first and second size-group, respectively) and on *Macrocystis* (77.61 and 97.27×10^{-5} g) (Fig. 4.28). Females raised on *Odonthalia* deposited the smallest egg masses (22.69 and 29.18×10^{-5} g). Paired multiple-comparisons analysis revealed that egg masses from females raised on *Hedophyllum* weighed significantly more than those from females raised on *Macrocystis* ($p < 0.05$), *Fucus*, *Iridaea* and *Odonthalia* ($p < 0.01$) (Fig. 4.28).

7

The average dry weight of egg masses deposited by *Lacuna vincta* correlated with the sizes of females and followed an exponential function ($r^2 = 0.945$) (Fig. 4.28). The regression equation relating the number of eggs to the dry weight of egg masses (Fig. 4.22) allowed an estimation of the average number of eggs per egg mass for the different groups of females after 45 days (Fig. 4.28). In the first size-group, females deposited egg masses containing: *Hedophyllum*: 1243 eggs, *Macrocystis*: 985 eggs, *Fucus*: 855 eggs, *Iridaea* 604 eggs, and *Odonthalia*: 270 (Fig. 4.28).

Figure 4.28. Relationship between average dry weight of egg masses and shell length of female *Lacuna vincta* raised on five intertidal algae. Turf: *Odonthalia floccosa* (13 and 22 egg masses for the first and second size-group, respectively); Irid: *Iridaea cordata* (43 and 36 egg masses); *Fucus*: *Fucus disticus* (54 and 28 egg masses); Mac: *Macrocystis integrifolia* (72 and 36 egg masses); Hedo: *Hedophyllum sessile* (84 and 66 egg masses). Points show mean dry weight (10^{-5} g) of egg masses. Error bars represent ± SD. Figure also shows calculated number of eggs contained in a typical egg mass.


Dry weight of egg masses
(10 -5 g)
160
120
80
40
0
3
4
5
6
Shell length (mm)
Turf
Fucus
Irid
Mac
Hedo
No. eggs
1678
1243
612
270

e. Estimation of the total fecundity between groups

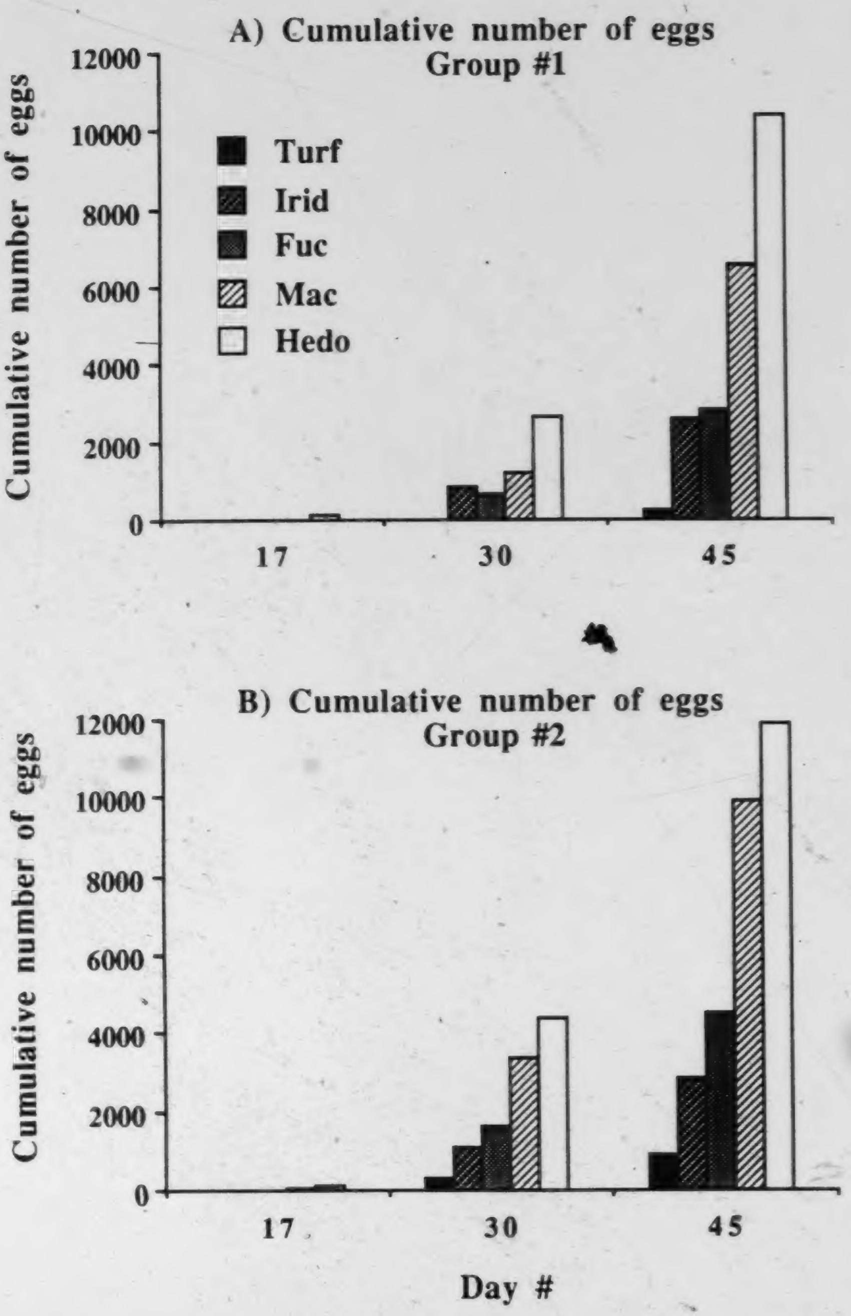
To estimate the total fecundity, the average cumulative dry weight of all egg masses deposited by each female of the different groups was determined and then converted into total number of eggs (Fig. 4.29 A, B). In the first size-group, females raised on Hedophyllum deposited an average of 10,356 eggs during the 45 days of the experiment. This contrasts markedly with only 232 eggs for female L. vincta raised on Odonthalia, thus representing only 2.2% of the those produced by females feeding on Hedophyllum (a 44-fold difference) (Fig. 4.29 A). Intermediate values were obtained for females raised on Iridaea and Fucus, with estimated total number of eggs deposited per female of 2565 and 2800 respectively. These values represent only 24.4% (Iridaea) and 27.0% (Fucus) of the average total number of eggs deposited by females raised on Hedophyllum (Fig. 4.29 A). Similar results were obtained with the second size-group of females (Fig. 4.29 B).

10. Short-term effects of diet shifts on size and fecundity of sexually mature Lacuna vincta

a. Maximal size of sexually mature females

Results from experiments in which sexually mature female Lacuna vincta (average shell length = 5.61 mm, SD = 0.361, n = 43) were transferred from Laminaria to four different algae and were raised for 36 days showed that algal shifts had a highly significant effect on growth and maximal size reached by adult females (from day 0 to 36; ANCOVA: differences among

Figure 4.29. Mean calculated cumulative number of eggs deposited per female *Lacuna vincta* raised on five intertidal algae after 17, 30 and 45 days of growth. Turf: *Odonthalia floccosa*; Irid: *Iridaea cordata*; Fucu: *Fucus disticus*; Mac: *Macrocystis integrifolia*; Hedo: *Hedophyllum sessile*. A) Size-group #1. B) Size-group #2.


A) Cumulative number of eggs
Group #1
Cumulative number of eggs
12000
10000
8000
6000
4000
2000
0
Turf
Irid
Fuc
Mac
Hedo
17
30
45
B) Cumulative number of eggs
Group #2
Cumulative number of eggs
12000
10000
8000
6000
4000
2000
0
17
30
45
Day #

slopes, $F = 26.854$, $p < 0.001$; among means $F = 7.512$, $p < 0.005$) (Fig. 4.30). Sexually mature female *L. vincta* transferred to *Hedophyllum* grew significantly, increasing by as much as 22.3% in shell length, (from 5.61 mm to 6.75 mm; Kruskal-Wallis ANOVA: $H = 23.99$, $p < 0.001$) (Fig. 4.30). In contrast, sexually mature females starting at the same size but raised on *Fucus*, *Iridaea* or *Odonthalia* for the same time period did not show any significant growth (*Iridaea*: $H = 5.70$, $p > 0.05$; *Odonthalia*: $H = 2.62$, $p > 0.05$; *Fucus*: $H = 3.87$, $p > 0.05$) (Fig. 4.30). Thus, these results indicate that growth and maximal size reached are optimal when sexually mature female *L. vincta* are fed on *Hedophyllum*.

b. Effect of changes in diet on colour of egg masses

An important observation was made during the experiments on diet shift. Female *Lacuna vincta* feeding on the brown algae *Laminaria*, *Hedophyllum* or *Fucus* produced white egg masses while those feeding on red algae like *Iridaea* or *Odonthalia* produced bright green egg masses (Fig. 4.31). Females recently transferred from a brown to a red alga, or from a red to a brown alga, deposited egg masses containing both colors, indicating rapid assimilation and elimination of pigments contained in their diet (Fig. 4.31). Twelve to 18 days after the diet shift, egg masses laid were the same color as those typically deposited by females that had been continuously feeding on that alga. During this study, white egg masses on *Iridaea*, green egg masses on *Hedophyllum* as well as green-white egg masses have been observed at the

Figure 4.30. Effect of algal choice on growth and maximum size of sexually mature female Lacuna vincta. Starting adult size: 5.61 mm; originally on Laminaria saccharina transferred to: H: Hedophyllum sessile; L: Laminaria saccharina; F: Fucus disticus; I: Iridaea cordata; T: turf alga (Odonthalia floccosa). Points show mean shell length (mm) of 11-22 groups of 2-4 females each. Error bars represent ± SD.

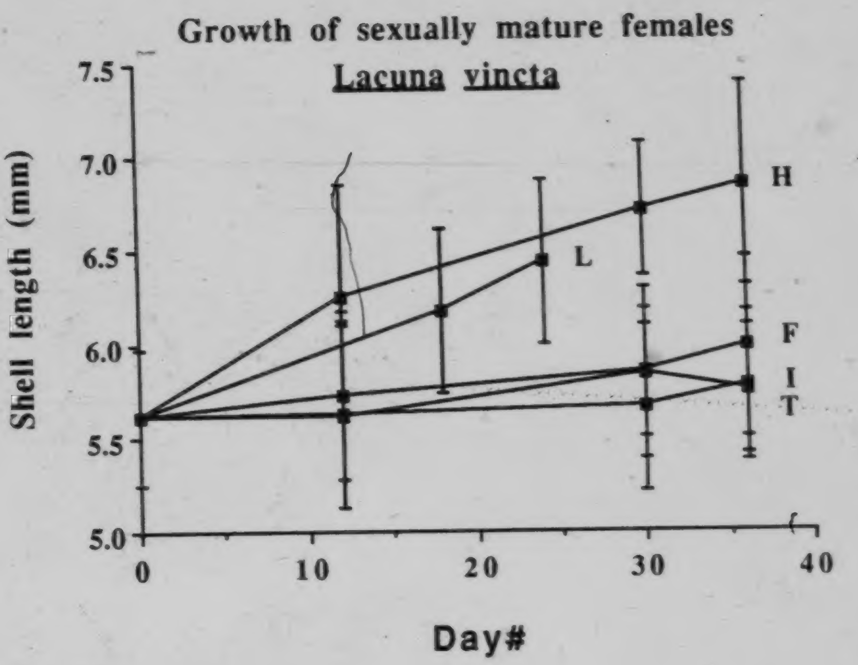
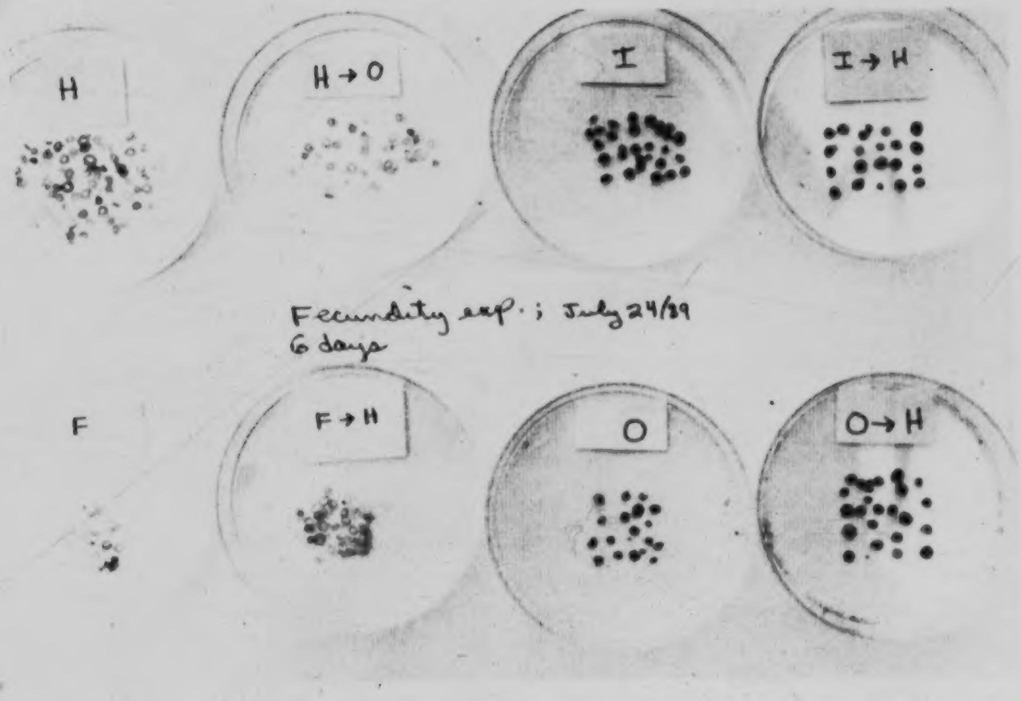

Growth of sexually mature females
Lacuna vincta
Shell length (mm)
7.5
7.0
6.5
6.0
5.5
5.0
0
10
20
30
40
Day#
H
L
F
I
T

Figure 4.31. Effects of recent algal shifts on fecundity and colour of egg masses of Lacuna vincta. Pictures show egg masses deposited by females (10 per group; originally from Laminaria saccharina) transferred to and raised on four algae during 18 days (Hedophyllum sessile (H), Odonthalia floccosa (O), Iridaea cordata (I) and Fucus disticus (F)). After day #18, females were tranferred once again onto a different alga: H to O, O to H, I to H and F to H and raised for another 6 days. Note the differences in number and colour of egg masses.


H
H→O
I
I→H
F
F→H
O
O→H

Fecundity exp.; July 24/39
6 days

study sites, therefore indicating that in the field adult *L. vincta* do shift between algae.

c. Spawning rate and dry weight of egg masses

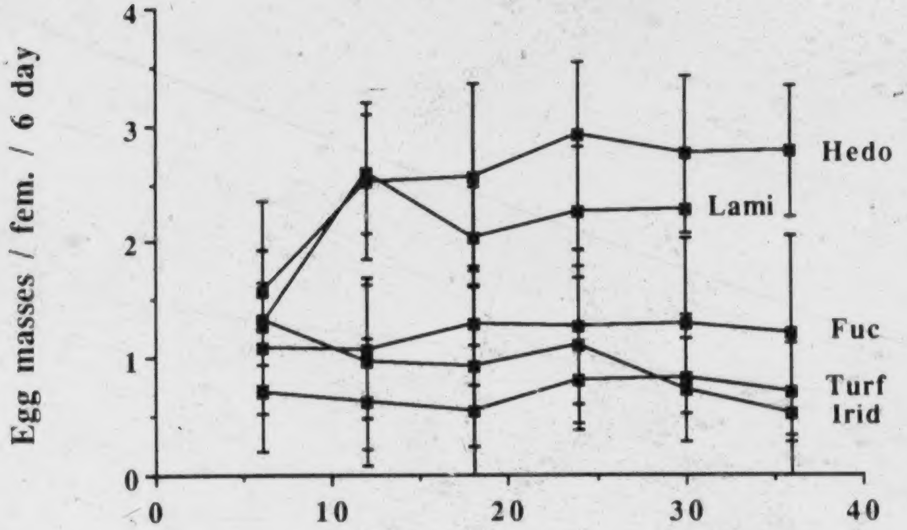
Sexually mature female *Lacuna vincta* feeding on *Laminaria* and transferred to other algae resulted in significant variations in fecundity occurring within 1 or 2 weeks after the transfer (Fig. 4.32). Spawning rates dropped by a factor of 2.37-4.09 only 12 days after a diet change from *Laminaria* to *Fucus*, *Iridaea*, or *Odonthalia* (0.617, 0.962, and 1.063 egg mass / female / 6 days, respectively) (One-way ANOVA: $F = 38.922$, $p < 0.001$) (Fig. 4.32 A). In contrast, spawning rates remained high in control snails on *Laminaria* as well as in females transferred to *Hedophyllum* (2.592 and 2.523 egg mass / female / 6 days) (Fig. 4.32 A).

Similarly, average dry weights of egg masses of females transferred to *Iridaea*, *Fucus* and *Odonthalia* were 38.4-62.7% lower than those on *Hedophyllum* and controls on *Laminaria*, being $50.32\text{-}85.12 \times 10^{-5}$ g after 18 days, compared to 137.55 and 124.19×10^{-5} g for *Hedophyllum* and controls, respectively (Kruskal-Wallis ANOVA, $H = 138.54$, $p < 0.001$) (Fig. 4.32 B).

Eighteen days after sexually mature female *Lacuna vincta* had been transferred from *Laminaria* to one of five species of algae, half the females of each group were transferred once again to a different seaweed. Significant decreases in fecundity occurred within only 6-12 days of this transfer (Figs. 4.33, 4.34). When compared to controls, the average spawning rate of females transferred from *Hedophyllum* to

Figure 4.32. Effects of recent algal shifts on fecundity of sexually mature female Lacuna vincta (originally on Laminaria saccharina). Turf: Odonthalia floccosa; Irid: Iridaea cordata; Fucu: Fucus disticus; Lami: Laminaria saccharina; Hedo: Hedophyllum sessile. A) Spawning rates (egg masses / female / 6 days). Points show mean spawning rate of 10-22 groups of 2-4 females each. B) Average dry weight of egg masses (10^{-5} g). Points show mean dry weight of 17-130 egg masses. Error bars represent ± SD.

A) Spawning rates



B) Average dry weight of egg masses

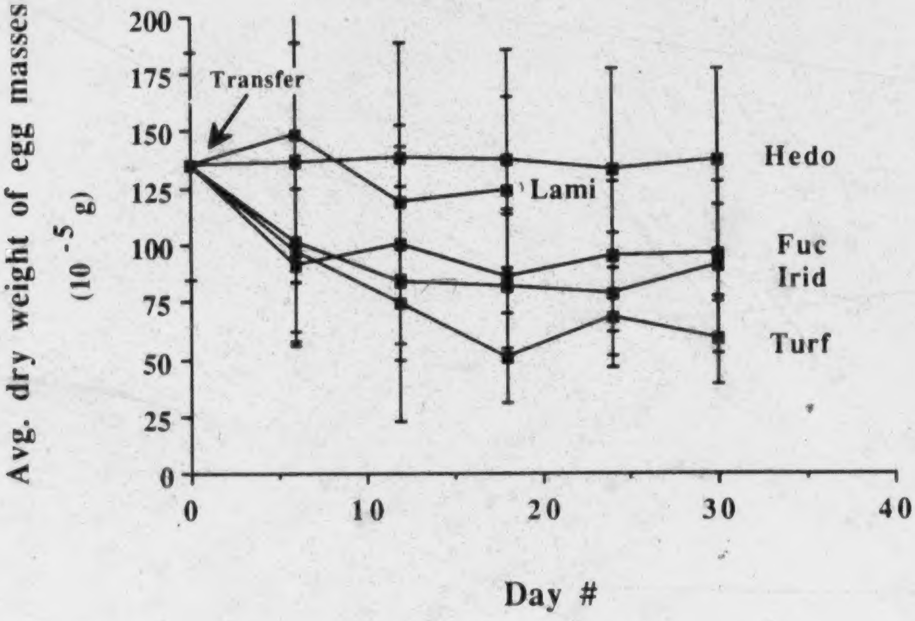


Figure 4.33. Effects of recent algal shifts on spawning rates of sexually mature female *Lacuna vincta* transfered to another seaweed after 18 days on a given diet (arrows indicate beginning of transfer). A) From *Hedophyllum sessile* to *Odonthalia floccosa*. B) From *O. floccosa* to *H. sessile*. C) From *Iridaea cordata* to *H. sessile*. D) From *Fucus disticus* to *H. sessile*. Points show mean spawning rate of 10-22 groups of 2-4 females each. Error bars represent ± SD.

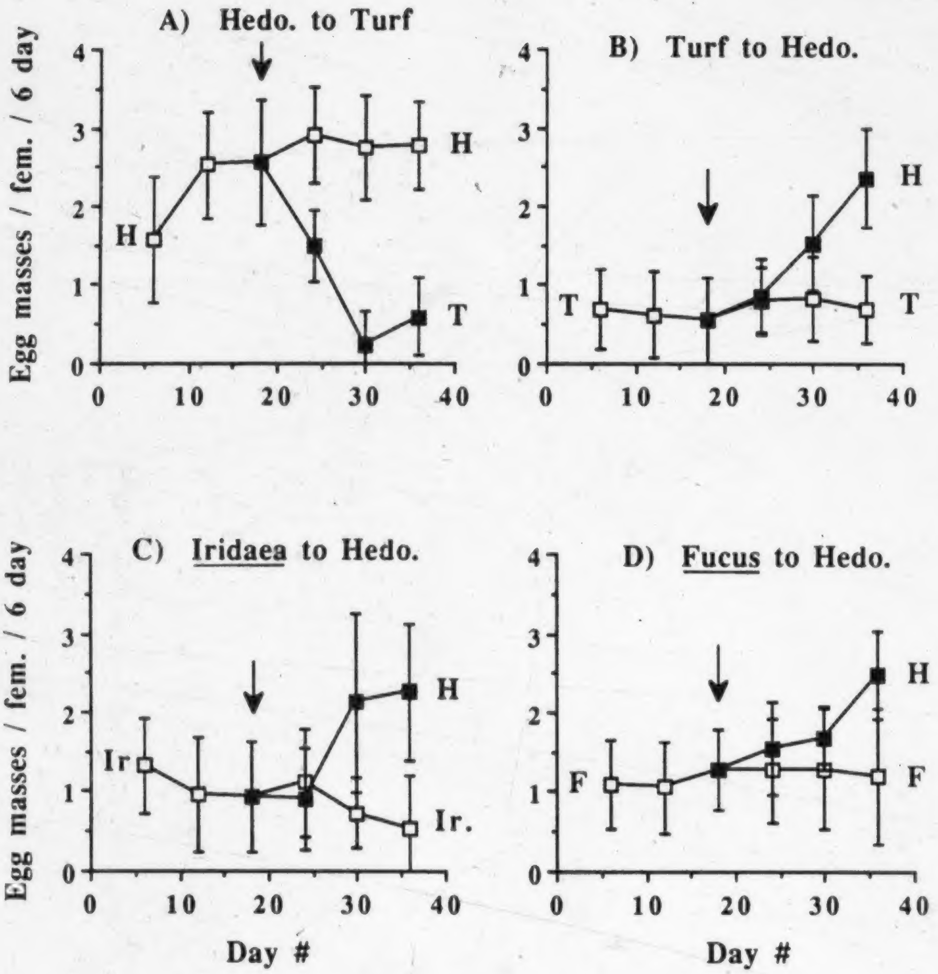
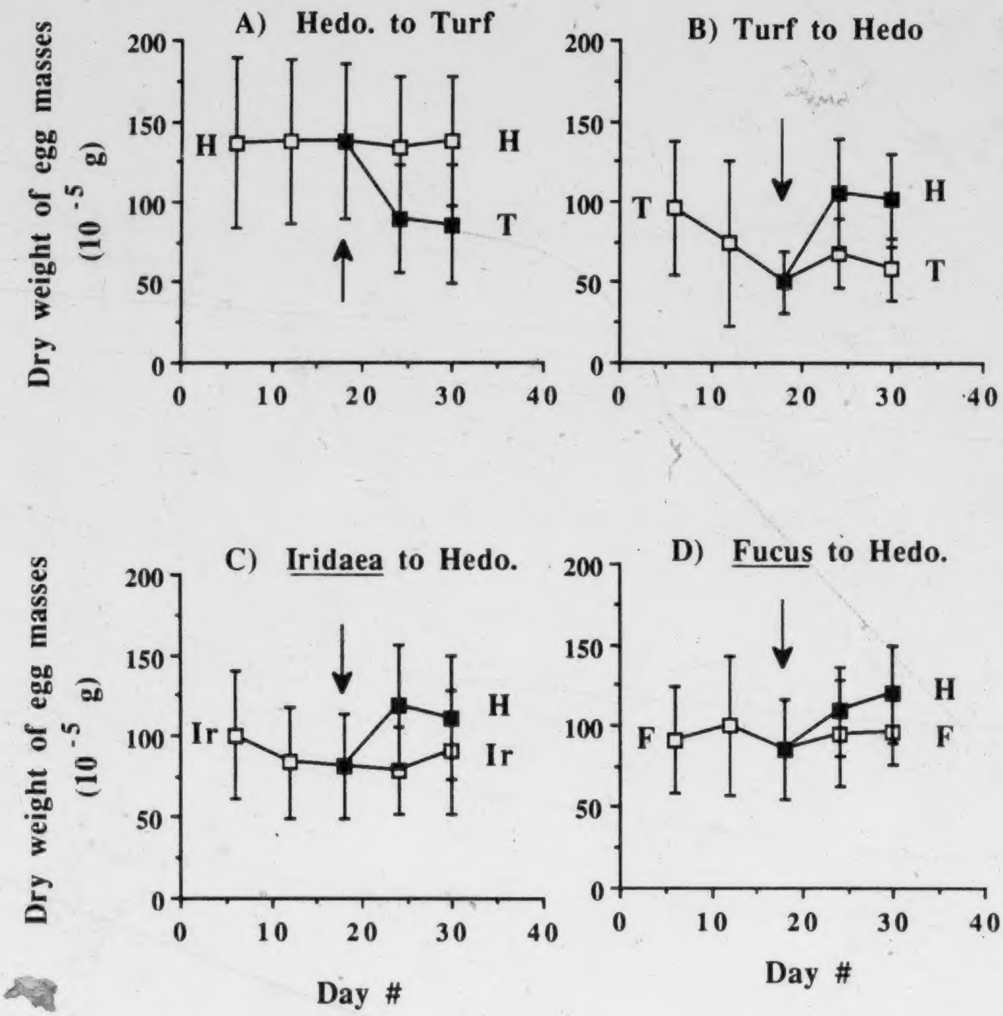

A) Hedo. to Turf
B) Turf to Hedo.
C) Iridaea to Hedo.
D) Fucus to Hedo.
Egg masses / fem. / 6 day
Day #
0
1
2
3
4
0
10
20
30
40
H
T
Ir
Ir.
F

Figure 4.34 Effects of recent algal shifts on dry weight of egg masses deposited by sexually mature female *Lacuna vincta* transfered to another seaweed after 18 days on a given diet (arrows indicate beginning of transfer). A) From *Hedophyllum sessile* to *Odonthalia floccosa*. B) From *O. floccosa* to *H. sessile*. C) From *Iridaea cordata* to *H. sessile*. D) From *Fucus disticus* to *H. sessile*. Points show mean dry weight (10^{-5} g) of egg masses (n = 17-130 egg masses). Error bars represent ± SD.


A) Hedo. to Turf
B) Turf to Hedo
C) Iridaea to Hedo.
D) Fucus to Hedo.
Dry weight of egg masses (10 -5 g)
Day #
0
50
100
150
200
0
10
20
30
40
H
T
Ir
F

Odonthalia dropped by as much as 48.5% within only six days after their transfer to Odonthalia, passing from 2.91 to 1.50 egg masses / female / 6 days (Mann-Whitney 2 Sample Test, $Z = 3.7632$, $p < 0.001$) (Fig. 4.33 A). Average dry weight of egg masses of these females in the above-mentioned transfer dropped by 37.5% during that period (6 days), passing from 137.15 to only 85.75×10^{-5} g ($Z = 4.986$, $p < 0.001$) (Fig. 4.34 A).

However, significant increases in fecundity occurred when female Lacuna vincta were transferred from Odonthalia to Hedophyllum (Figs. 4.33 B, 4.34 B). The average spawning rate increased by as much as 84.3% within 12 days of the transfer (0.83 compared to 1.53 egg masses / female / 6 days; $Z = -2.208$, $p < 0.05$) and by more than 200% 18 days after this transfer (from 0.53 to 2.26 egg masses / female / 6 days) (Fig. 4.33 B). Furthermore, the average dry weight of egg masses from the same females increased by as much as 54.1% only six days after the transfer (68.06 compared to 104.88×10^{-5} g; $Z = -3.4733$, $p < 0.001$) (Fig. 4.34 B).

Similar increases in fecundity occurred 6-12 days after Lacuna vincta were transferred from Iridaea to Hedophyllum, with the spawning rate increasing by as much as 190% after only 12 days (Mann-Whitney 2 sample test, $Z = 2.8461$, $p < .001$) (Fig. 4.33 C). Average dry weights of egg masses increased by 51.1% after only six days ($Z = -3.7826$, $p < 0.001$) (Fig. 4.34 C). Finally, those females transferred from Fucus to Hedophyllum doubled their spawning rate 18 days after the transfer, passing from 1.20 to 2.48 egg masses / female / 6 days (Mann-Whitney 2 Sample Test, $Z = 3.1616$, $p < 0.005$) (Fig. 4.33 D).

d. Effect of recent algal shifts on total egg production

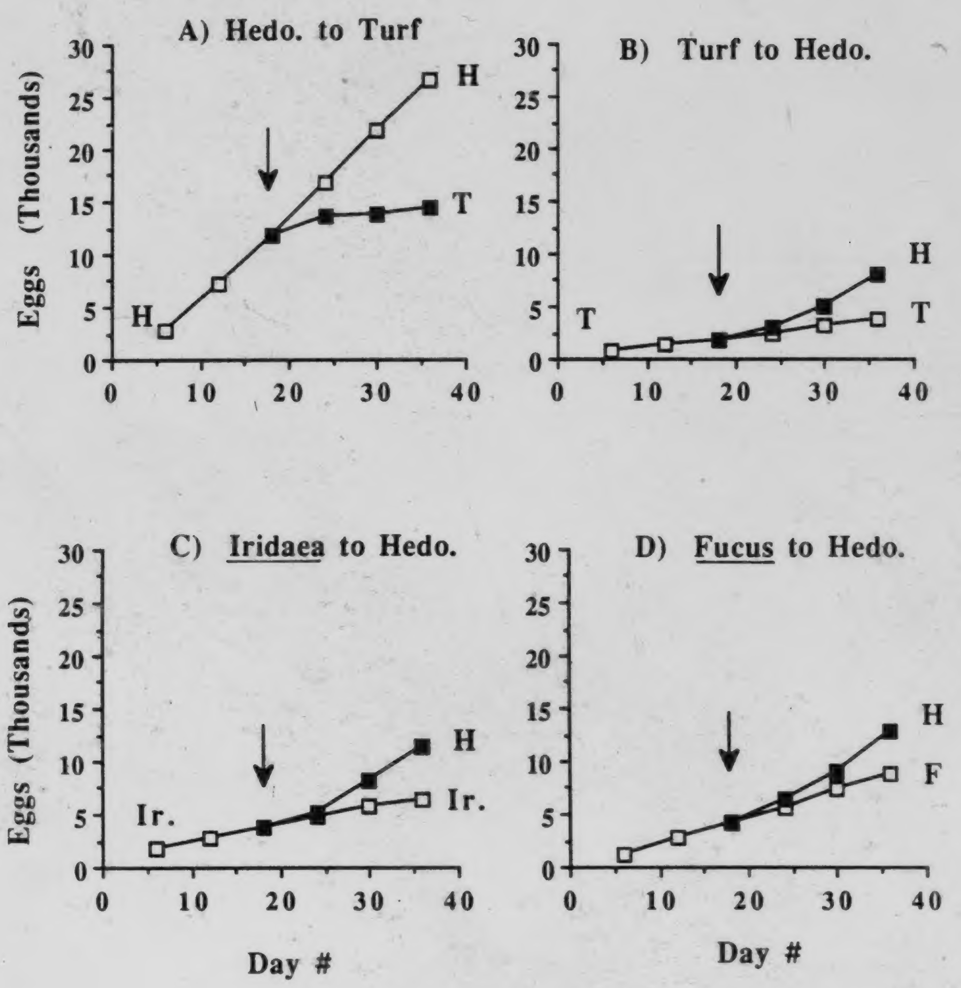
The cumulative number of eggs produced was calculated to estimate the overall effect of substratum / diet shifts on fecundity of sexually mature female Lacuna vincta (Fig. 4.35). Results indicate that egg production decreased by as much as 19.6, 36.5 and 45.7% after 6, 12 and 18 days, respectively, when females were transferred from Hedophyllum to Odonthalia (Fig. 4.35 A).

In contrast, those transferred from Odonthalia to Hedophyllum deposited 17.9, 57.7 and 118.6% more eggs after 6, 12 and 18 days, respectively (Fig. 4.35 B). Egg production of females transferred from Iridaea to Hedophyllum and from Fucus to Hedophyllum increased by 88.7% and 45.1%, respectively, after 18 days (Fig. 4.35 C, D).

D. DISCUSSION

Abundance of Lacuna vincta and L. variegata on Hedophyllum and Iridaea at Prasiola Point follows an annual cycle, fluctuating seasonally. The analysis of size-frequency distributions indicated that these gastropods complete their life-span in one year and recruit onto seaweeds in large numbers year after year. Similar results were obtained in previous studies on the population biology of intertidal Lacuna spp. conducted in different geographical

Figure 4.35. Effects of recent algal shifts on calculated total number of eggs deposited by sexually mature female *Lacuna vincta* transfered to another seaweed after 18 days on a given diet (arrows indicate beginning of transfer). A) From *Hedophyllum sessile* to *Odonthalia floccosa*. B) From *O. floccosa* to *H. sessile*. C) From *Iridaea cordata* to *H. sessile*. D) From *Fucus disticus* to *H. sessile*. Points show calculated number of eggs (based on Figs. 22, 32 and 33).


A) Hedo. to Turf
B) Turf to Hedo.
C) Iridaea to Hedo.
D) Fucus to Hedo.
Eggs (Thousands)
Day #
0
5
10
15
20
25
30
0
10
20
30
40
H
T
Ir.
F

regions (Smith, 1973; Southgate, 1982 a; Langan, 1984; Grahame, 1986).

Field observations and laboratory experiments indicated that both Lacuna vincta and L. variegata subsist on a variety of algae. Other studies reported similar findings (Smith, 1973; Fretter and Manly, 1977; Southgate, 1982 a; Grahame, 1986). Lacuna's habitat encompasses seaweeds from a wide range of biochemical compositions, morphologies as well as structural complexities, and includes brown, red and green algae.

Despite their plasticity in habitat selection, both Lacuna vincta and L. variegata choose certain algae preferentially. The abundance and distribution of these snails also vary ontogenetically and seasonally. Although large juvenile and adult L. vincta and L. variegata are abundant on Hedophyllum and Iridaea, respectively, their larvae settle in much higher numbers on structurally more complex substrata like red turf algae. The structural complexity of the plant is a determining factor in the density of Lacuna spp. veligers settling and metamorphosing on a particular algae in semi-exposed intertidal rocky shores.

In the present study it was impossible to concentrate on all species of algae used by Lacuna spp.. Emphasis has been placed on several seaweeds on which the life stages, from settling larvae to adults, typically occur at Prasiola Point.

1. Settlement of *Lacuna* spp. larvae on semi-exposed intertidal seaweeds: the importance of plant structure and complexity

a. Structurally-complex substrata

Turf algae are important settlement habitats for *Lacuna* spp. larvae. These finely-branched red algae harbour high numbers of newly-metamorphosed juveniles (most < 2 mm), with densities of snails up to 6 times higher than that on *Hedophyllum*. Fretter and Manly (1977) as well as Southgate (1982 a) reported high settlement rates of *L. vincta* larvae in similar semi-exposed turf algal communities along the coasts of England.

At Prasiola Point, juveniles of the gastropod *Tricolia pulloides*, *Barleeia* spp. and *Lacuna* spp. were abundant on red turf algae (Martel, unpublished; see Chapter III). The abundance of small herbivorous and detritivorous gastropods in semi-exposed turf algae has been reported (Bishop and Bishop,1973; Wigham, 1975; Fretter and Manly, 1977; Borja, 1986). Similarly, small bivalves, including numerous species of clams, *Mytilus* spp., as well as brooding *Musculus* sp. and *Lasaea* sp., were common on red turf algae (see Chapter III). *Mytilus* spp. larvae are known to settle heavily on structurally complex substrata, including red turf algae (Bayne, 1964; Paine, 1976; Eyster and Pechenik, 1987). These bivalves remain attached to the algae by means of their byssus. Drifting invertebrates found in off-bottom collectors made with the turf alga *Gracilaria* were also dominated by small juvenile gastropods and bivalves (see Chapter III). These findings suggest that red turf algae constitute an important nursery habitat for larvae and juveniles of numerous species of molluscs (see Bishop and Bishop, 1973).

Several factors may determine the elevated densities of small-sized molluscs, including the larvae and newly-metamorphosed juvenile Lacuna spp., on the structurally-complex red turf algae. In their study on the settlement of gastropod larvae on seaweeds, Fretter and Manly (1977) proposed that red turf algae provide a rich supply of epiphytic diatoms on which post-larvae and newly-metamorphosed juveniles feed. Epiphytic diatoms are usually found in higher densities on red turf algae than on the bladed seaweeds such as Hedophyllum and Iridaea (Martel, unpublished). Detritus, which is often ingested by juvenile Lacuna spp. accumulates on turf algae (Fretter and Manly, 1977; Smith et al., 1985; Martel, unpublished). Marx and Herrnkind (1985) as well as Herrnkind and Buttler (1986) reported that post-larval and juvenile Panulirus (spiny lobster) use subtidal red turf algae as a nursery. They indicated that such habitats likely harbour food items required by these early life stages and provide protection from fish predation. In addition, Coull and Wells (1983) showed that the use of structurally-complex red coralline algae by intertidal copepods can significantly reduce predation by fish.

The ability of the red turf alga Gelidium nudifrons to modify the hydrodynamic conditions (turbulence of water flow) has been reported by Anderson and Chartel (1982). Favourable hydrodynamic conditions created by the fine branches of red turf algae may contribute to the high settlement rates of gastropod and bivalve larvae as well as to the abundance of their juvenile stages in this habitat. Yet, the effects of hydrodynamics, plant shape and substratum complexity on the recruitment of larvae and abundance of juvenile gastropods and bivalves remain relatively unknown (but see Eckman, 1987).

b. Low settlement of Lacuna spp. larvae on intertidal kelp

A conspicuous characteristic of the population biology of Lacuna spp. is its low settlement rate on Hedophyllum at Prasiola Point during the spring (despite blades being covered with bullae at that time). This markedly contrasts with the situation observed in the red turf algae. During April, advanced L. vincta veligers were abundant in the plankton (see Chapter II), but larval settlement was very low to nil on Hedophyllum. It was not before mid- to late May that significant recruitment, realized by the arrival of various sizes of juvenile Lacuna spp. (most snails between 1 and 3 mm), began to occur on this kelp.

Field observations in semi-exposed low intertidal Laminaria groendlandica beds when competent Lacuna spp. larvae were abundant in the plankton also confirmed the very low rates of larval settlement directly on kelp blades. Similarly, settlement rates of *Lacuna* spp. larvae in off-bottom *Hedophyllum* collectors indicated that this seaweed trapped significantly fewer larvae than did those made of *Gracilaria pacifica*. The cause of this discrepancy remains unknown. Vahl (1971) reported a similar situation in the limpet *Patina pellucida* living on the low intertidal kelp *L. hyperborea* in western Norway. He mentioned the absence of direct larval settlement on this kelp and noted that only large juvenile (≥ 3 mm) and adults were present on the plant. He postulated that the time lag between larval settlement and recruitment of juvenile limpets on the kelp could be explained by the limpet larvae settling and metamorphosing on other substrata before migrating to the adult habitat. Vahl (1971) proposed that the kelp was an unsuitable settlement substratum for the limpet larvae. He suggested that the newly-metamorphosed juvenile limpets had a diet different from that of larger individuals, and that they could not rasp the thick cell walls of *Laminaria*. The primary habitat, however, selected by the larvae of this limpet, was not specified.

Comparisons of stomach contents of *Lacuna* spp. eating different algae support Vahl's hypothesis of an ontogenetic shift in diet between post-larvae/newly-metamorphosed juveniles and larger individuals. Diatom frustules were found in the stomachs of newly-metamorphosed juveniles living on red turf algae, while plant cell walls were found in stomachs of both juveniles and adults living on *Hedophyllum* (Martel, unpublished). Padilla (1985) demonstrated that a greater force was required by a limpet to rasp the cell wall of *Iridaea* and *Hedophyllum* than to rasp that of crustose red algae. It is possible that only juveniles of a certain age or size can feed on the cell walls of *Hedophyllum*. This topic will need to be elucidated in future research.

It is also possible that settling larvae and newly-metamorphosed juveniles have difficulties remaining attached to the alga. In comparison with the foot area, the frontal area of the shell of juvenile *Lacuna vincta* is proportionally larger than that of adults (Martel, unpublished). Vahl (1971) showed that the ratio shell height/aperture area of the limpet *Patina pellucida* decreased from 0.30 for individuals 1-2 mm shell length to only 0.06 for adults (6 mm). In addition, Branch and Marsh (1978) reported that drag coefficients in limpets increase with decreasing size. Since tenacity is a function of foot area (Miller, 1974) a size-related difference in the ratio of frontal to foot area could indicate that newly-metamorphosed individuals are more subject to being dislodged than larger ones (but see Warburton, 1976).

The foot of larvae or recently-metamorphosed individuals may not be fully developed and thus may be unable to adhere efficiently to the smooth surfaces of kelp blades. The thick layer of mucilage on kelp blades could also contribute to weaker adhesion. In addition, laboratory experiments on crawling behaviour of different size-groups of Lacuna vincta on kelp blades established that, contrary to large individuals, newly-metamorphosed juveniles remained stationary at high (25+ cm / s) velocity flows (Martel, unpublished).

2. Recruitment of Lacuna spp. on bladed algae: the importance of post-metamorphic drifting and blade morphology

a. Post-metamorphic drifting in intertidal Lacuna spp.

Size-frequency distributions of Lacuna spp. at Prasiola Point during the spring (1987 and 1988) revealed that the recruitment of these snails on Hedophyllum is accomplished by the arrival of juveniles, and not larvae. There was no evidence of mass movements of snails towards Hedophyllum by crawling. Juveniles (1-2 mm shell length) arrived several weeks after the peak larval settlement. The high numbers and the similarity in size-frequency distributions of Lacuna spp. found in off-bottom intertidal collectors at the same time substantiate that these juveniles had arrived on Hedophyllum by drifting (also see Chapter III). In addition, 34-42% of all individual Lacuna spp. trapped daily in off-bottom collectors during the spring had a shell length > 1 mm. These results thus substantiate the key role played by post-metamorphic drifting in the recruitment and population dynamics of Lacuna spp. in semi-exposed intertidal seaweed communities.

The arrival of large juvenile and adult *Lacuna* spp., via drifting, onto seaweeds used by adults during spawning, as is observed on *Hedophyllum* during the late fall, may explain the increase in density of snails reported by Southgate (1982 a), Langan (1984) and Grahame (1986). Yet, drifting as the mechanism of this immigration was not investigated in their studies. However, Johnson and Mann (1986) reported that *Lacuna vincta* living in subtidal *Laminaria longicruris* beds in Nova Scotia drift in the water column and rapidly invade kelp blades that had been previously cleared of snails.

Post-metamorphic drifting has been shown to play an important role in the dispersal and recruitment of bivalves (Bayne, 1964; Sigurdsson *et al*., 1976; de Block and Tan-Maas, 1977; Prezant and Charlermwat, 1984; Lane *et al*., 1985; Beukema and de Vlas, 1989). Vahl (1971) mentioned that juveniles of the limpet *Patina pellucida* migrate to the adult habitat (*Laminaria*) by drifting. He later mentioned the importance of mucus in this process (see Vahl, 1983). I established in Chapter III that mucous threads greatly enhance the drifting snail's ability to attach to nearby substrata.

b. Significance of blade morphology on abundance of snails

At Prasiola Point, seasonal changes in blade morphology of *Hedophyllum* markedly affected density of *Lacuna* spp. on the plant. In late spring/early summer, when *Hedophyllum* blades were bullated, snail densities sharply increased and numerous juveniles were found in the bullae. The importance of bullae as shelters was clear when comparing abundance of snails on flat blades and bullated blades. Numbers of Lacuna spp. were 1-2 orders of magnitude higher on bullated blades than on flat blades. An analogous pattern was observed when comparing abundances of Lacuna spp. on individual Hedophyllum blades which were half-bullated and half-flat. At the end of the summer, as Hedophyllum blades became flat, densities of Lacuna spp. dropped to minimal values.

An important conclusion of this study is that the sudden disappearance of juvenile snails from a particular seaweed need not necessarily be associated with mortality. Post-metamorphic drifting was potentially responsible for the sharp decreases in density of Lacuna spp. reported in previous studies (see Smith, 1973; Fretter and Manly, 1977; Grahame, 1986). In the present study, however, the fate of the vast numbers of snails that disappeared from Hedophyllum at the end of the summer is, as yet, unascertained. Considering the ability of Lacuna spp. to drift with its mucous thread, it is conceivable that a large proportion of these juveniles succeeded in recolonizing other algae.

Widdowson (1965) mentioned that the bullated and flat (smooth) Hedophyllum morphs represent different stages in the development of the same individuals. He also speculated that these variations correlated with changing environmental factors. The physical appearance of Hedophyllum is known to vary considerably between regions. Bullated plants are characteristic of sheltered areas with low wave action, while smooth and flat plants occur in more exposed areas (Abbott and Hollenberg, 1976). More recently, Armstrong (1987) studied the mechanical properties of Hedophyllum tissue from both exposed and protected sites. She did not mention, however, the seasonal changes in blade morphology occurring in semi-exposed or exposed sites that are reported in the present study.

The effect of microhabitats and shelters, including pits and crevices, on the abundance and size-frequency distribution of rocky intertidal gastropods has been demonstrated (Raffaelli and Hughes, 1978; Reimchen, 1979; Hughes and Roberts, 1981; Gosselin and Bourget, 1989). Emson and Faller-Fritsch (1976) demonstrated that juvenile L. rudis use empty barnacles as microhabitats but move to natural rock crevices as they outgrow the barnacles. They also reported a 5- to 8-fold increase in the density of this snail when artificial pits and holes were created in the bedrock, suggesting that the abundance of these gastropods is limited by the availability of crevices and similar shelters. In these studies, it was suggested that the use of such microhabitats is an adaptation preventing animals from being dislodged by wave-action. Black (1976) reported that juveniles of the limpet Acmaea insessa living on the kelp Egregia laevigata recruit preferentially in pits and depressions created by adults grazing on the plants.

In intertidal habitats subject to crashing waves or to strong surge, gastropods likely find protection in pits, bullae or other microhabitats. Studies on water flow above rough surfaces have shown that water flow can "skim" above the irregularities of the substratum, leaving the animals residing inside in "dead water" (Morris, 1955, cited in Davis, 1986). The use of such microhabitats by gastropods could allow the animal to minimize the likelihood of accidental dislodgement when exposed to full force flow (see Vogel, 1981; Denny *et al.*, 1985; Denny, 1988). On the other hand, the use of bullae (and folds in the winter) by *Lacuna* spp. could also reduce predation risks by fish (see Chapter II). The exact reason for the use of such microhabitats by intertidal *Lacuna* spp. remains to be elucidated.

c. Winter increase in density on *Hedophyllum*: evidence of algal shifts accomplished by mature snails

Abundance of *Lacuna* spp. on *Hedophyllum* peaked during late spring as well as during late fall/early winter. In the fall, however, *Hedophyllum* blades were flat. Snails were usually found at the base of the plant, as well as inside folds at the edges of blades. It is possible that the grazing of *Hedophyllum* plant cell walls by large individuals in the winter induces or promotes the curling of the blade and the formation of folds, and thus shelters, which are typically used by *L. vincta* at that time. This problem warrants further investigations.

Size-frequency distributions indicated that the late fall/winter increase was caused by immigration of large juveniles and adults, particularly of *L. vincta*. Similar increases in *L. variegata* density also occurred on *Iridaea*, and there too, most snails arriving were large juveniles and sexually mature individuals. Interestingly, Langan (1984) reported similar increases in density of large individuals (> 2 mm shell length) of *L. marmorata* and *L. unifasciata* on *Phyllospadix* in California. In addition, Southgate (1982) mentioned that although newly-hatched juvenile *L. pallidula* were found in large numbers on turf-like red algae, the adult population and egg masses were largely restricted to the brown alga *Fucus serratus*. This suggested the occurrence of a migration of juveniles back to the adult habitat. This pattern of habitat use reported by Southgate for *L. pallidula* is remarkably similar to that reported in the present study between red turf algae and *Hedophyllum*. High numbers and size-frequency distributions of *Lacuna* spp. found in off-bottom collectors during November of 1988 suggested that these increases were the result of immigration of large individuals by drifting (particularly *L. variegata*), although the data presented here cannot entirely refute the potential arrival by crawling. On the other hand, the patchy, sparse distribution of many intertidal seaweed species during winter could present a serious obstacle for these gastropods.

The increase in density of *Lacuna vincta* on *Hedophyllum* during late fall/early winter, coincided with a decrease in their abundance on other types of seaweeds, such as *Halosaccion* (Figs. 4.14, 4.15). Therefore, these findings suggest that *L. vincta* migrates from certain algae toward others, such as *Hedophyllum*, prior to the breeding season. Such algal shifts could play an important role in the life history of *L. vincta* considering that many seaweeds used by juveniles during the spring and summer become scarce or disappear during the winter. In contrast, algae like the long-lived *Hedophyllum* remain abundant and represent more persistant habitats where *L. vincta* can overwinter, spawn and complete its life cycle.

In addition, it was documented in the present study that diet shifts can affect the colour of egg masses, with white egg masses deposited when snails feed on brown algae and green egg masses deposited when they feed on red algae. White *Lacuna vincta* egg masses on *Iridaea*, green egg masses on *Hedophyllum* as well as green-white (both colours) egg masses have been observed at the study sites, thus confirming that diet (therefore substratum) changes do occur in the field.

Lacuna's dynamic pattern of habitat-use is not only influenced by changes in algal preferences during ontogeny, but is also affected by seasonal variations within the populations of algae used by the snails. Post-metamorphic drifting plays a governing role in this system by enabling individuals to move effectively between the different components of its habitat. As shown in this study, substratum choices made by drifting snails have dramatic consequences on life-history parameters.

3. Long-term effects of algal choice by larvae and juvenile *Lacuna* spp. on life-history parameters

In the context of certain life-history traits observed in *Lacuna* spp. -- including a short life-span and a comparatively long period of egg-laying -- findings from the present study indicate that substratum choice made by settling larvae and particularly by drifting juveniles and adults has marked consequences on growth rates and, more importantly, on the total reproductive output and therefore overall fitness of the snails.

a. Effects of algal choice on growth rates and adult size

Newly-metamorphosed *Lacuna vincta* living and feeding on *Nereocystis* and *Macrocystis* grew faster and reached larger sizes than those raised on *Ulva* or red turf algae. Females raised on kelp were nearly twice the size, at age six months, of those of the same age raised on *Ulva* or on a mixture of three red turf algae (Fig. 4.20). Similar results were obtained with males, although the difference was less pronounced.

Parallel conclusions were drawn from experiments in which five different seaweeds used by *Lacuna vincta* at Prasiola Point were tested for their effects on the growth of juvenile (2.72-3.20 mm) *L. vincta*. Growth rates of juveniles were much higher for individuals raised on *Hedophyllum*, a typical adult habitat, compared with juveniles raised on *Fucus* or *Iridaea*. Also, lower growth rates were consistently obtained when juveniles were raised on the red turf alga *Odonthalia*. Female *L. vincta* raised on *Hedophyllum* grew by 82.1-91% after 45 days, contrasting with only a 12.7-24.9% increase for those raised on *Odonthalia*. Similarly, growth rates of newly-metamorphosed *L. variegata* on *Odonthalia* were consistently lower than on bladed algae (e.g., *Iridaea*, an alga typically used by adult *L. variegata*). One would have expected higher growth rates on red turf algae and *Odonthalia*, since they are used extensively by settling larvae and newly-metamorphosed juvenile *L. vincta* and *L. variegata*.

These results imply that juvenile *Lacuna vincta* on bullated *Hedophyllum* blades during late spring/early summer at Prasiola Point should show high growth rates for the time the plants remain bullated. Yet, the study of size-frequency distributions and cohorts of *Lacuna* spp. on *Hedophyllum* at that time indicated growth rates were slow (see Fig. 4.7 A, B). A plausible explanation is the high turnover of individuals in the bullae. Arrival of juveniles finding shelter in the bullae of *Hedophyllum* could be balanced by departures of individuals that have been present inside the bullae. Juveniles could have reached sizes exceeding the depth of the protective bullae and emigrated from the plant. The foundations of this hypothesis are three-fold: (1) high numbers and similar size-frequency distributions of juvenile Lacuna spp. drifting during May of 1988 as well as those found inside the bullae of Hedophyllum at that time; (2) faster growth of snails on flat blades during late summer/fall -- as suggested by the analysis of size-frequency distributions (see Fig. 4.7 A, B); (3) constant growth rates of Lacuna spp. on Iridaea, which lacks bullae (see Fig. 4.17 A, B, C). Experiments involving the release and recapture of marked snails living in the bullae of Hedophyllum would shed more light on this hypothesis.

b. Long-term effects of algal choices on reproductive responses

The species of alga fed to juvenile Lacuna vincta had pronounced effects on their subsequent reproductive output. The lifetime fecundity of adult females raised from newly-metamorphosed juveniles (< 1 mm) on kelp (Nereocystis and Macrocystis) was more than one order of magnitude higher than that of females that had been raised on Ulva or on three red turf algae. Smith (1973) estimated that, in the field, an average Lacuna vincta living on Fucus serratus deposits approximately 13.4 egg masses, for a calculated total of 16,163 eggs. Findings from the present study indicate values nearly twice that high when females are raised on kelp (see Grahame [1977, 1982] for data on energetics and reproductive output in Lacuna).

In addition, laboratory experiments on the reproductive output of female Lacuna vincta raised from large juveniles

(2.60-2.80 mm and 3.15-3.20 mm shell length) on five intertidal algae at Prasiola Point confirmed the existence of a close relationship between the type of alga on which individuals are raised and their fecundity. Juvenile female *L. vincta* raised on *Hedophyllum* deposited twice as many egg masses after 45 days as did females raised on *Iridaea* or *Fucus*, and nearly eight times as many as those raised on *Odonthalia*. Moreover, the average dry weight of egg masses deposited by females raised on *Hedophyllum* was twice that of egg masses deposited by females raised on *Fucus* and *Iridaea*, and more than four times that of those from females feeding on *Odonthalia*.

Finally, the total number of eggs produced after 45 days indicated that females raised on *Hedophyllum* deposited 2-4 times more eggs than those raised on *Fucus* or *Iridaea*, and 10 times more eggs that females raised on *Odonthalia*. Differences in growth rates and maximum sizes reached between females raised on different algae, coupled with the exponential relationship between the size of females and the average dry weight of egg masses, are mainly responsible for the diet-related variation in fecundity.

Size-related sexual dimorphism in *Lacuna vincta* has been reported in previous studies (Smith, 1973; Southgate, 1982a). I demonstrated that diet, and thus habitat, can markedly affect the extent of this size-related sexual dimorphism in *L. vincta*. It was more pronounced when *L. vincta* were fed kelp (*Macrocystis*, *Nereocystis* or *Hedophyllum*) than when fed other seaweeds (e.g. Fucus, Iridaea, Ulva or Odonthalia). In addition, females raised on kelp reached larger sizes and deposited larger egg masses. Field observations of Lacuna vincta living on Hedophyllum at Prasiola Point showed a sexual dimorphism 50% greater than those living on Fucus in Grappler Inlet. Although the possibility of a location effect exists in this comparison -- the two groups of snails were from two different sites -- it is possible that the type of alga on which these snails were feeding was the main factor responsible for this variation.

Because of the positive correlation between fecundity and female size, pronounced sexual dimorphism may represent a mechanism by which individuals take advantage of optimal food conditions and maximize reproductive output.

4. Short-term growth and reproductive responses of sexually mature female Lacuna vincta following diet changes

Sexually mature female Lacuna vincta transferred from Laminaria onto Hedophyllum grew significantly (22.1% increase) after 36 days, while those transferred onto Fucus, Iridaea or Odonthalia did not. These results support field observations in suggesting that sexually mature female L. vincta can reach maximal sizes when living on this kelp.

Rapid changes in reproductive output of sexually mature female Lacuna vincta follow diet changes. Fecundity can be significantly altered just 6-12 days after transfer from one seaweed to another. These changes were expressed in terms of spawning rates as well as in terms of dry weight of egg masses and, therefore, total number of eggs per spawn. Sexually mature female L. vincta feeding on Hedophyllum produced 19.6% and 36.5% less eggs, respectively, only 6-12 days after having been moved to Odonthalia. The opposite trend, however, occurred within 6-18 days after females had been transferred from Iridaea, Fucus or Odonthalia, to Hedophyllum. Female L. vincta fed Hedophyllum had consistently higher spawning rates and produced larger egg masses than females on other algae.

The cell walls of the different groups of seaweeds mentioned in the present study are known to contain varying types and amounts of carbohydrates (Percival and McDowell, 1981). It is possible that certain carbohydrates contained in kelp enable herbivorous invertebrates, including Lacuna vincta, to maximize their growth and fecundity. Gremare et al. (1988) mentioned, however, that reproductive outputs in the polychaete Capitella sp. were better explained by the organic nitrogenous contents of the diet than by the organic carbon content or total calories. The specific composition of the constituents affecting growth and fecundity of L. vincta remain to be elucidated.

The effect of food quality on egg production has been the object of studies on insects (see review by Scriber and Slansky, 1981) and in planktonic organisms (Ambler, 1986; Arnott et al. 1986 and others) but little attention has been given to such experimental assessments in marine benthic invertebrates other than polychaetes (polychaetes: Levin, 1986; Levin and Creed, 1986; Gremare *et al*., 1988; Qian, 1989 a, b). Several studies have focused on the effects of food on somatic and gonadal growth in clams (Epifanio, 1979) and scallops (Grant and Cranford, 1989; MacDonald and Thompson, 1985 a, b; Barber *et al*. 1988). Himmelman (1984) reported that the urchin *Strongylocentrotus droebachiensis* prefers certain kelp species, such as *Laminaria* and *Alaria*. Although they are grazed, red algae are not preferred, and somatic and gonadal growth are significantly lower when urchins are fed these algae rather than kelp. According to Raymond and Scheibling (1987), juvenile *S. droebachiensis* originally feeding on crustose red algae and switched to *Laminaria* showed significant increases in both somatic and gonadal tissues compared with natural controls feeding on crustose red algae. The present study is, to my knowledge, the first detailed report on the effects of different natural diets on growth, reproductive output and lifetime fecundity of a marine gastropod.

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CHAPTER V.

GENERAL CONCLUSION

The recruitment of the herbivorous gastropod *Lacuna vincta* in the canopy of *Macrocystis* and *Nereocystis* beds in Barkley Sound has been examined. Four factors influencing the intensity and patterns of recruitment were studied, namely: seasonal pattern of spawning (oviposition), larval abundance, growth of larvae in the plankton and larval settlement. By studying the cohorts and the growth of *Lacuna* spp. veligers in the plankton prior to the spring recruitment an estimate of the time the larvae spend in the plankton (7-9 weeks) and their size at metamorphosis (700-850 um) was obtained. The study of cohorts of larvae also enabled the forecasting of the timing and intensity of recruitment.

Patterns of abundance of advanced larvae (> 500 um) in the plankton and recruitment rates in kelp canopies were found to follow similar trends. One of the characteristic features of *L. vincta* populations found in *Macrocystis* and *Nereocystis* canopies in Barkley Sound is the dominance of newly-metamorphosed juveniles and the absence of adult stages. This contrasts with subtidal and low intertidal populations of *L. vincta*, where peak spring recruitment in the kelp canopy is followed by a rapid decline in juvenile density. These results suggest that newly-metamorphosed juvenile *L. vincta* remain in the canopy habitat for a short period of time and then migrate toward the benthic undercanopy and low intertidal seaweeds. Migration is accomplished by drifting in the water column by means of a mucous thread. I hypothesized that the lack of shelter for growing juveniles and an increased vulnerability to fish predation are the causes of this habitat shift.

In the present thesis, I report that species other than Lacuna, including a neogastropod (Alia sp.) and at least one unidentified species of asteroid, are also found as newly-metamorphosed juveniles in the canopy habitat. Kelp bed canopies could function as larval collectors and could be exploited by many benthic marine invertebrates of the shallow subtidal and low intertidal benthic communities as a nursery habitat.

Dispersal via drifting in several marine benthic invertebrates lacking a planktonic larval stage is demonstrated through the use of off-bottom intertidal collectors. These collectors were mimics of an algal habitat commonly used by small molluscs in the intertidal seaweed community. Dispersal is accomplished by juveniles (and even sexually mature adults in the case of small-sized species) drifting with water currents. Some of these drifting invertebrates have been caught in collectors placed offshore, in the middle of a bay. These findings indicate that, contrary to what is suggested by their mode of development, these invertebrates have alternative and likely effective dispersal mechanisms -- at least at the local scale. Interestingly, the drifting species lacking a planktonic larval stage all have wide geographical distributions in the eastern Pacific region. It is probable that frequent drifting excursions enhance rafting opportunities, which in turn may favor long distance dispersal.

Large numbers of juveniles of several other species of molluscs whose life cycles include a planktonic larval stage were also caught in off-bottom collectors. Thus juvenile drifting is a common feature of the life history and ecology of many small bivalves and gastropods, regardless of their mode of development.

An important scientific contribution of the present study is the demonstration that drifting in _Lacuna_ spp. can be initiated by the animal. Macrocinematographic video recordings revealed that _Lacuna_ spp. can quickly produce a mucous thread and initiate drifting when exposed to water flows (particularly oscillating currents). The animal raises the metapodium -- regardless of the orientation of the snail with respect to the orientation of the water flow -- until most of the sole's surface no longer contacts the substratum (only the most anterior [propodial] region remains fixed). At that time, the mucus produced and accumulated at the posterior of the sole of the foot is taken away with the water current, and stretched up to 160 times the length of the animal. The mucous thread pulled by water currents then transports the animal, enabling it to drift in an almost neutrally buoyant fashion.

In Lacuna spp., the production of a mucous thread also greatly reduces sinking rates in snails. While extension of the foot and antennae are not effective in reducing the sinking rate. In addition, early juvenile stages of other gastropod species, although not recognized as adapted for drifting in the water column, can, when dislodged, produce sufficient mucus to reduce their sinking rates significantly. One of the most important functions of mucous threads is to increase the drifting animal's ability to obtain rapid contact with, and attachement to, nearby substrata. This was particularly well demonstrated for L. vincta in a flow tank.

I have also shown that two taxonomically unrelated gastropods capable of drifting, produce mucous threads of similar structure. Drifting threads, such as those produced by Lacuna spp. and Barleeia spp. (two of the most common drifters found in collectors) are microscopic and are comprised of numerous parallel fibers. This pattern of organization is likely responsible for the stretching capability of these drifting threads and markedly differs from that of non-drifting attachment mucous threads produced by other gastropods also living on seaweeds. In Alia gouldi, a neogastropod that produces a mucous thread used as an anchoring device, at least two types of fibers are present. The fibers are coiled in a complex fashion and likely give strength, rather than elasticity, to the thread.

In rocky intertidal seaweed communities the planktonic larvae of Lacuna vincta and L. variegata settle on various algae. Settlement rates are particularly high on structurally-complex substrata like the red turf algal community, perhaps due to favorable hydrodynamic conditions prevailing within such algae and/or ontogenetic differences in food preferences by these snails. In contrast, settlement rates on bladed algae commonly used by large juvenile and adult *L. vincta* during spawning, e.g. *Hedophyllum*, are extremely low. Spring recruitment on *Hedophyllum* occurs several weeks after the peak larval settlement period and is accomplished by juvenile drifting.

Plant morphology, and the presence of shelter such as pits and bullae on the surface of *Hedophyllum* blades, are major determinants of patterns of abundance of juvenile *Lacuna* spp. on this kelp. Abundance of juvenile *Lacuna* spp. on *Hedophyllum* during the spring and summer at Prasiola Point coincided with the presence of bullae on the blades. Moreover, it was demonstrated that rapid declines in juvenile density on this kelp during the summer may not necessarily be due to massive mortality, but simply the result of emigration or habitat shift accomplished by drifting, following changes in blade morphology and thus the disappearance of these microhabitats on the kelp blades.

Substratum (algae) choice made by larvae at settlement and particularly by juvenile and adult *Lacuna* spp. during drifting has significant implications for life-history parameters of the individuals. Although newly-metamorphosed juveniles are found in high density on structurally-complex seaweeds (e.g. red turf algae), growth rates in such habitat are low. In addition, snails raised on such algae reach small adult sizes and have a low lifetime fecundity. Growth rates, maximum adult size, as well as egg production in L. vincta increase noticeably when juveniles or adults leave the substratum originally selected at settlement and emigrate to kelp such as Hedophyllum. When raised on Hedophyllum, juvenile L. vincta reach much larger sizes than those raised on red algae, and size-related sexual dimorphism is also more pronounced. An exponential relationship exists between the weight of egg masses and the size of the females. Because spawning rates (egg masses / female / week) of females raised on Hedophyllum are very high, the total reproductive output -- expressed in terms of total number of eggs deposited -- of females raised on the kelp can be more than one order of magnitude higher that of females raised on algae originally selected at settlement. Thus, individuals that drift away from turf algal settling grounds and colonize other algae can markedly enhance their lifetime fecundity.

Sexually mature female Lacuna vincta that have already reached adult size (e.g. 5^+ mm) and started spawning, can still grow significantly and increase their fecundity if they drift and colonize brown algae like Hedophyllum. Indeed, the reproductive output of sexually mature females that migrate or drift to Hedophyllum can be increased within 6-18 days of colonization of the kelp, depending on the type of alga from which they originate. Field observations of colour of L.

vincta egg masses -- which is influenced by diet -- found on various intertidal seaweeds, coupled with comparisons between size-distributions and seasonal abundance of *L. vincta* on various species of seaweeds, confirmed that emigration from certain red algal communities (eg. *Halosaccion*) to *Hedophyllum*, accomplished by large juveniles and adults, does occur. In addition, contrasting with annual or perennial seaweeds used by *Lacuna vincta*, *Hedophyllum* is long-lived and represents a persistent habitat where this snail can overwinter, spawn and complete its life cycle.

The risks associated with drifting excursions have not been addressed. Nonetheless, because of the complexity and the seasonality of intertidal algal habitats, results obtained in this study strongly suggest that dispersal via drifting of post-metamorphic stages is adaptive in *Lacuna* sp.. Post-metamorphic drifting allows these short-lived gastropods to move effectively between algae and to utilize juvenile and adult habitats optimally, enabling them to eventually colonize more persistent algae and maximize their reproductive fitness before senescence.